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Systematics of the Smooth-Toothed Pocket Gopher, *Thomomys umbrinus,* in the Mexican Transvolcanic Belt

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ABSTRACT

Difficulties in the subspecific identification of more than 200 specimens of *Thomomys umbrinus* from the State of Tlaxcala led us to examine the systematic status of the eight subspecies recognized within the Mexican Transvolcanic Belt. We gathered representative samples of those subspecies (≥ 50) during three years of fieldwork. These were analyzed together with samples from other populations not previously assigned to subspecies, as well as voucher specimens from several collections. Thirty-seven variables, obtained from 1145 specimens, were analyzed morphometrically using univariate and multivariate statistics. Within-population variation was highly influenced by sexual dimorphism, and especially by ontogenetic variation; therefore, these two factors should be considered carefully when making systematic and taxonomic decisions. Our analysis of geographic variation determined only two recognizable subspecies of *Thomomys umbrinus* within the Mexican Transvolcanic Belt: *Thomomys umbrinus umbrinus* (Richardson, 1829) and *Thomomys umbrinus pullus* Hall and Villa, 1948.

RESUMEN

Dificultades en la identificación subespecífica de más de 200 especímenes de *Thomomys umbrinus* del estado de Tlaxcala, nos llevaron a examinar el estado sistemático de las ocho subespecies reconocidas en el Eje Volcánico Transversal. Obtuvimos muestras representativas de esas subespecies (≥ 50) durante tres años de trabajo de campo. Estas fueron analizadas junto con muestras de otras poblaciones no asignadas previamente a las subespecies y ejem-

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plares de referencia de varias colecciones. Treinta y siete variables fueron obtenidas de 1145 ejemplares y fueron analizadas morfométricamente utilizando estadística uni y multivariada. La variación intrapoblacional resultó altamente influenciada por el dimorfismo sexual, pero especialmente por la variación ontogenética; por ende, estos dos factores deben ser considerados cuidadosamente cuando se tomen decisiones sistemáticas y taxonómicas. Nuestro análisis de la variación geográfica determinó que sólo pueden reconocerse dos subespecies de *Thomomys umbrinus* en el Eje Volcánico Transversal: *Thomomys umbrinus umbrinus* (Richardson, 1829) y *Thomomys umbrinus pullus* Hall y Villa, 1948.

INTRODUCTION

A large and highly heterogeneous sample of *Thomomys umbrinus* from Tlaxcala included the whole variety of diagnostic characters for the eight subspecies acknowledged in the MTB, Mexican Transvolcanic Belt, (Nelson and Goldman, 1934; Hall and Villa, 1948). In fact, the Tlaxcalan specimens could be assigned to any of the following subspecies: *Thomomys umbrinus albigularis* from Hidalgo; *Thomomys umbrinus martinensis* and *Thomomys umbrinus orizabae* from Puebla; or *Thomomys umbrinus vulcanius* from México (Hall, 1981).

Examination of most of the holotypes and topotypes of the subspecies from the MTB housed at National Museum of Natural History (USNM) and the American Museum of Natural History (AMNH), made clear the qualitativeness of the diagnostic characters. For example, *Thomomys umbrinus, vulcanius, T. u. tolucae, T. u. martinensis, T. u. umbrinus*, *T. u. albigularis*, and *T. u. peregrinus* are similar both in shade and in cranial characteristics. In fact, some *T. u. albigularis* lack the allegedly diagnostic white spot on their throat (Nelson and Goldman, 1934), but some *T. u. peregrinus* and all of those of *T. u. vulcanius* do have it. In *T. u. orizabae*, the holotype and most of the topotypes differ from the preceding by their melanic shade; however, melanic individuals were also found among Tlaxcalan specimens as well as in *T. u. pullus* collected in Michoacán.

Those qualitative characters, together with the apparently isolated distribution of the populations along the MTB, were previously used in designating seven of the eight subspecies in the MTB (Merriam, 1893; Bailey, 1915; Nelson and Goldman, 1934). Since only small sample sizes (n ≤ 15) were examined, investigators emphasized a geographic but not necessarily a genetic isolation nor a wider morphological variation.

Therefore, we decided to allocate the Tlaxcalan specimens according to the morphometric variation of the subspecies within the MTB, expecting that our results would motivate a thoughtful study of variation in this taxon throughout its range. Such scope would enable greater comprehension of the systematics and taxonomy of *Thomomys umbrinus* in the MTB. It might also contribute to a better understanding of the role of subspecies as a means of recognizing geographic variants of the species (Mayr, 1969). This is possible if the subspecies is regarded as conspecific populations sharing their genetic pool through gene flow (Smith and Patton, 1988; Patton and Smith, 1989), on one hand, but which have a particular morphometric variation because they are adjusted to the habitat conditions in their geographic area (Grinnell, 1935; Yates and Schmidly, 1977; Honeycutt and Schmidly, 1979; Patton and Smith, 1990).

After three years of fieldwork, we gathered large sample sizes (n ≥ 50) along the MTB. In addition, voucher specimens from the MTB were examined in several collections. Qualitative examination of collected and voucher specimens showed that persistence of morphological features was not consistent within a particular locality; on the contrary, the variation was generally noticeable. The only exception was the distinctly small-sized specimens of *T. u. pullus*. Moreover, in addition to the overlapping morphological variation among the samples from MTB, standard karyotypes and allozymic data showed no distinctions among some of them (Hafner et al., 1987). That is, *T. u. pullus* (Pátzcuaro, Michoacán), *T. u. tolucae* (Toluca, México), *T. u. vulcanius* (Amecameca, Estado de México), and *T. u. umbrinus* (Boca de Monte, Veracruz) belong to the same chromosomic (NF = 78) and allozymic groups (Hafner et al., 1987). These data together certainly do not suggest distinct species, and perhaps not even separate subspecies.

Therefore, the objective here was to examine geographic variation among the populations of *Thomomys umbrinus* in the Mexican Transvolcanic Belt. Morphometric analyses include the eight previously recognized subspecies and populations not previously allocated from the states of México, Michoacán, and Tlaxcala.

DIAGNOSTIC CHARACTERS, TAXONOMY, AND DISTRIBUTION OF *THOMOMYS UMBRINUS*

Thomomys umbrinus is a rodent species of fossorial habits belonging to the Geomyinae within the Geomyidae. The genus is characterized (Hall, 1981) by its small size and by the rather delicate structure of its hands with fine claws, as opposed to the robust hands with strong claws of other genera (*Geomys* and *Cratogeomys*). The genus *Thomomys* does not show the basitemporal fossa located between the lower third molar (m3) and the lingual face of the coronoid process is rather a slight depression in some specimens in the United States. *Thomomys* has the front surface of the upper incisors smooth, but with a very fine groove toward the inner limit, while the other genera of the family have either one (*Cratogeomys*, *Pappogeomys* and *Zygogeomys*) or two well-defined (*Orthogeomys*) grooves. In addition, the third upper molar (M3) is elliptic, monoprismatic, and similar to the other two upper molars (M1, M2) in *Thomomys*. Conversely, in other genera the M3 is rather biprismatic and differs from the M1 and M2 (Hall, 1981).

Within the genus, systematic and taxonomic status of *Thomomys umbrinus* has undergone numerous changes (Hall and Kelson, 1959; Anderson, 1966; Hoffmeister, 1969; Patton and Dingman, 1968; Patton, 1973; Hall, 1981; Ramírez-Pulido et al., 1996). Such changes include: (1) synonymy with other congeneric species (Bailey, 1915; Hall and Kelson, 1959; Hall, 1981) and (2) recognition of *Thomomys bottae* and *T. townsendii* as separate species (Anderson, 1966; Hoffmeister, 1969; Patton and Dingman, 1968; Patton, 1973; Patton and Smith, 1990). Furthermore, changes include the subsequent reorganization of the involved subspecies.

Before conclusive evidence was gathered (Patton and Dingman, 1968; Patton, 1973; Patton and Smith, 1990) to formally consider them as separate species (Patton, 1993), Hall (1981) combined *Thomomys umbrinus* with *Thomomys bottae* and included 229 subspecies. Therefore, the distribution of *Thomomys umbrinus* started north of the United States and extended along the Californian mountain ridges and the Sierra Madre Occidental and Sierra Madre Oriental, all the way down to the MTB.

The distribution is discontinuous, particularly in the states of the Mexican Plateau and the MTB. The presence of arid zones and, probably, the presence of some species of *Cratogeomys* (Hall, 1981) have contributed to this pattern. Indeed, Nelson and Goldman (1934) noted that *Cratogeomys merriami merriami* restricted the distribution of *Thomomys* at 11,500 ft in the Popocatepetl Volcano, and that *Cratogeomys tylorhinus planiceps* did the same at 8600 ft in the Nevado de Toluca Volcano. Observations by Nelson and Goldman (1934) were confirmed during fieldwork, especially in the Valley of México, where *Cratogeomys* occurs in many localities in which *Thomomys umbrinus* is no longer found.

Simpson (1961) strongly criticized the large number of subspecies allocated to *Thomomys umbrinus* (Smith and Patton, 1988), and in so doing, he placed this taxon in the midst of a debate on the validity of the subspecies (Grinnell, 1935; Davis, 1938; Wilson and Brown, 1953; Brown and Wilson, 1954; Simpson, 1961; Choate and Williams, 1978; Smith and Patton, 1988; Patton and Smith, 1990). In fact, studies by Patton et al. (Patton, 1973; Patton and Feder, 1978; Hafner et al., 1987) have raised new questions about the taxonomic and systematic population status of this species. Hafner et al. (1987) found three chromosomic groups within *Thomomys umbrinus* that show genic differentiation at the allozymic level, suggesting more than one species of pocket gopher as currently recognized.

After the separation of *Thomomys umbri-*

nus and *Thomomys bottae*, 47 subspecies from the 78 occurring in Mexico (Hall, 1981) have been allocated to the latter (Patton and Smith, 1990; Patton, 1993; Ramírez-Pulido et al., 1996). Therefore, *T. umbrinus* is represented by the remaining 31 subspecies which occur along the Sierra Madre Occidental from southern Sonora downward to Durango and Nayarit. In the Mexican Plateau, the species is distributed in patchy arrangements in Chihuahua and Coahuila in the north but in more isolated populations in Zacatecas, Aguascalientes, San Luis Potosí, and Guanajuato in the center. In the Sierra Madre Oriental, *T. umbrinus* extends from mid-Coahuila to Nuevo León. The species was reported to occur in the MTB within isolated populations in Michoacán, México, Distrito Federal, Morelos, Tlaxcala, Puebla, Hidalgo, and Veracruz (Hall, 1981).

The eight subspecies occurring in the MTB (Hall, 1981) are *Thomomys umbrinus umbrinus* (Richardson) in Veracruz; *Thomomys umbrinus orizabae* Merriam in Puebla; *Thomomys umbrinus peregrinus* Merriam in Distrito Federal, Hidalgo, México, and Morelos; *Thomomys umbrinus albigularis* Nelson and Goldman in Hidalgo, Puebla, and Veracruz; *Thomomys umbrinus martinensis* in Puebla; *Thomomys umbrinus tolucae* Nelson and Goldman in the state of México; *Thomomys umbrinus vulcanius* Nelson and Goldman in México, Morelos, and Puebla; and *Thomomys umbrinus pullus* Hall and Villa in Michoacán.

STUDY AREA

The Mexican Transvolcanic Belt (MTB) includes the highest regions of México (2000 to 5650 m), located between 19° and 20°N and 96° and 105°W, and crossing the country from ocean to ocean. From west to east, the volcanoes related to this study are Nevado de Toluca (4624 m), Popocatepetl (5452 m), Iztaccihuatl (5460 m), La Malinche (4461 m), and Pico de Orizaba (5700 m). The region is 130 km deep and more than 1000 km long. It is bounded by the Sierra Madre Oriental in the east, by the Sierra Madre del Sur in the south, and by the Sierra Madre Occidental in the west. There are about 1000 volcanoes from the Quaternary Age of less than 1 million years (Fa and Morales, 1991, Demant, 1978; Nixon et al., 1987; Pasquaré et al., 1987a, 1987b) in the MTB.

Specimens were collected in the second through fifth districts recognized by Demant (1978) in the MTB. The second district in the east shows numerous monogenetic cones and, except the Tancítaro Hill in Michoacán, there are no stratified volcanoes. Four large stratified volcanoes are located from the third to the fifth districts at the center of the MTB (Nevado de Toluca, Popocatepetl, Iztaccíhuatl, and La Malinche) and oriented in a north-south direction within the lake depression corresponding to the Sierra Nevada. Other small sierras, among which Chichinautzin is found, run in a northeast-southwest direction, on fissures closer to the southernmost portion of the Valley of México. In the fifth district, the Cofre de Perote-Pico de Orizaba volcano chain, which is a recent lava cone on an older volcano, runs eastward.

The sampled zones have a temperate climate with rainfall at the end of spring and fall, and the northern portions are less humid than their southern counterparts. The annual average temperature is generally about 18°C, but it decreases as altitude increases (García, 1981). The predominant vegetation in the studied areas (Rzedowski, 1978) is oak forest (*Quercus* sp.), pine-oak (*Quercus-Pinus* sp.) and pine-spruce (*Pinus-Abies religiosa*) as well as pine forest with fodder grass (*Muhlenbergia* sp. and *Festuca* sp.). Because the parent rock is volcanic, the ground is sandy near the volcanic uplifts and more clayey in the lower regions.

METHODS

COLLECTING AND EXAMINING SPECIMENS

Previously, specimens from the study area were less than 15 in most collections and no extensive morphometric work had been conducted. Therefore, we decided to collect intensively and to examine voucher specimens in several mammal collections. After three years of exhaustive fieldwork, more than 50 representative samples of most of the recognized subspecies were obtained from the type locality and neighboring areas. The two exceptions were *T. u. martinensis* (n = 47) and *T. u. umbrinus* (n = 5). Specimens were also collected from unsampled areas between populations of the recognized subspecies in the states of of México, Tlaxcala, and Michoacán. Such samples suggest gene flow among all populations of *Thomomys umbrinus* in the MTB. In total, 857 specimens were gathered from 67 localities in the states of Hidalgo, México, Michoacán, Morelos, Puebla, Tlaxcala, and Veracruz. The collected specimens were prepared as skins and skulls (Hall, 1981; Ramírez-Pulido et al., 1989) and they are housed at Colección de Mamíferos de la Universidad Autónoma Metropolitana, Unidad Iztapalapa (UAMI). The skulls were cleaned with dermestid beetles (Hall and Russell, 1933; Ramírez-Pulido et al., 1989).

In addition, 288 specimens from nine localities, were examined in other collections: Colección de Mamíferos del Laboratorio de Cordados Terrestres, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (CB) at México City; American Museum of Natural History (AMNH) at New York; National Museum of Natural History, Smithsonian Institution (USNM) at Washington, D.C.; Texas Cooperative Wildlife Collections (TCWC) of the Texas A&M University in College Station; Museum of Natural History (KU) of the University of Kansas, Lawrence. Among specimens in other museums, most holotypes (USNM) and several topotypes (AMNH, CB, KU, UAMI) of the mentioned species were examined. Exceptions include the holotype of *Thomomys umbrinus pullus*, at the University of Michigan, and that of *Thomomys umbrinus umbrinus*, at the Natural History Museum, London.

We examined 1145 specimens of *Thomomys umbrinus* from 76 localities in the six mentioned states. However, the number of specimens included varied with the type of statistical analysis. In addition, some very young specimens or damaged skulls were eliminated. The numbers of specimens in each calculation is mentioned in the methods or in the tables for each study.

Sex of most specimens was gathered from museum catalogs and labels. In the few cases in which sex was unrecorded, the skins were examined for evidence such as well-developed scrotum or nipples. The pelvic structure was also checked for sexual differences (i.e., a larger pubic foramen and a wider simphysis in females); however, if the postcranial skeleton was not available, the specimen was excluded.

Hair color of holotypes, topotypes, and other specimens (n = 76, 55♀; 21♂) was reviewed. We looked for qualitative taxonomic characteristics that might distinguish the subspecies. Likewise, in order to obtain data about the habitat and the exact capture localities, the original collectors' notes on the specimens were reviewed. Among others, notes of W. Dalquest in 1946 (KU), S. Anderson in 1952 (KU), and E. W. Nelson in 1892 (USNM), were examined.

MEASUREMENTS

Four conventional external measurements (Hall, 1981) together with 33 skull measurements (fig. 1) were recorded from each specimen. The external measurements are the total length of the body (TOL); length of the vertebral tail (LVT); length of the right hind foot (HFT); and length of the ear (LOE). Measurements were taken from the skin labels of voucher specimens.

Some skull measurements were taken from the literature (Thaeler, 1968; Heaney and Timm, 1983) and others were suggested by Dr. Michael Smolen (Texas A&M University, Nov. 1989). However, most measurements were selected during direct examination of the specimens by one of us (ACC). Cranial measurements (fig. 1) were taken with calipers and recorded to the nearest 0.01 mm. The following list contains the names and abbreviations of measurements (numbers in parentheses correspond to fig. 1).

BRAINCASE AND ROSTRUM

GLS	(1–1′) greatest length of skull
LNA	(1–2) length of nasals
LMX	(2′–2″) length of maxilla
LFO	(3–3′) length of frontal
LZA	(4–4′) length of zygomatic arch
LBC	(4–5) length of braincase
ICO	(6–6′) interorbital constriction
WRO	(7–7′) width of rostrum
AZB	(8–8′) anterior zygomatic breadth
MZB	(9–9′) medial zygomatic breadth
PZB	(10–10′) posterior zygomatic breadth

SBP	(11–11′) skull breadth across parietals (i.e., braincase)
LDI	(12–12′) length of diastema
LMT	(12–13) length of molar toothrow
LPF	(14–14′) length from the pterygoid fossa to the basioccipital
BAM	(15–15′) breadth across molars (M1-M1)
BAB	(16–16′) breadth across bullae
BOP	(17–17′) breadth across basioccipital processes
HRO	(18–18′) height of rostrum
HMC	(19–19′) height of maxillary crests
MHS	(20–20′) maximum height of skull
HBP	(21–21′) height from the bulla to the parietal

Mandible

BCP	(22–22′) breadth across coronoid processes
BJT	(23–23′) breadth across jaw teeth (m2-m2)
AWD	(24–24′) anterior width of dentary
GWM	(25–25′) greatest width of mandible
MWD	(26–26′) medial width of dentary
GLD	(27–27′) greatest length of dentary
LCP	(28–28′) length to coronoid process
BML	(28–29) basal mandible length
DHI	(27–30) dentary height from basis of incisive alveolum
AHM	(28–31) anterior height of mandible
PHM	(29–28′) posterior height of mandible

Sampled Localities

Sampling was carried out within: (a) localities represented by few specimens ($n < 50$); (b) localities in potential corridors for gene flow among previously recognized subspecies; (c) localities still occupied by *Thomomys umbrinus*; or (d) topotypic localities of subspecies not represented in Mexican collections (i.e., *T. u. albigularis, T. u. martinensis, T. u. orizabae, T. u. pullus, T. u. tolucae,* and *T. u. umbrinus*).

In the field, we noticed that *T. u. albigularis, T. u. pullus,* and *T. u. martinensis* were becoming scarce at the type localities. This rarity results from habitat modifications and from displacement by *Cratogeomys merriami*. In fact, only one topotypical female of *T. u. albigularis* from the National Park ‘‘El Chico,’’ at the Sierra de Pachuca, Hidalgo, was collected and most of the 58 inividuals of *T. u. pullus* were collected at Los Tanques, Michoacán. We collected no specimens of *T. u. martinensis* at San Martin Texmelucan, State of Mexico, during the three years of fieldwork. Fortunately, 40 individuals referable to *T. u. martinensis* were located at the USNM.

Nelson and Goldman (1934) described *Thomomys umbrinus orizabae* and, especially, *T. u. tolucae* and *T. u. vulcanius* with imprecise localities. Therefore, our sampling was conducted as close as possible to the localities described in the fieldnotes. Accordingly, specimens of *T. u. orizabae* were examined from Miguel Hidalgo y Costilla, Puebla. In the state of México, we collected specimens of *T. u. tolucae* at several localities near the Nevado de Toluca Volcano, and the same was done with *T. u. vulcanius* at the Paso de Cortés.

Sampled localities (SL) are mapped in figure 2 and are detailed under Examined Specimens. Samples of *Thomomys umbrinus* collected in zones not previously recorded, but which were in the gaps between two recognized subspecies, are considered to be vouchers for corridors of genetic continuity between the eight subspecies inhabiting the MTB (fig. 2).

Nongeographic Variation

Individual variation, ontogenetic variation, and sexual dimorphism were examined in the population of the Sierra de Tlaxco, Tlaxcala ($n = 356$). We considered four age groups (1 = young; 2 = subadults; 3 = adults; 4 = old specimens) among 214 females and 142 males according to the expansion of the zygomatic arches and the elongation of the rostrum relative to the braincase (Castro-Campillo et al., 1993).

Individual variation in each external and cranial measurement was analyzed by obtaining the standard statistics (mean, $\bar{x}$; standard error, SE; minimum value, MIN; maximum value MAX; coefficient of variation, CV) with the routine PROC UNIVARIATE SAS (SAS, 1985). These analyses also served to corroborate the normal distribution of the data and helped in finding outlier values.

We determined ontogenetic or age variation and the presence of secondary sexual dimorphism for each taxonomic character, through a one-way analysis of variance with ANOVA routine. When significant differences ($p < 0.05$) between ages or sexes were

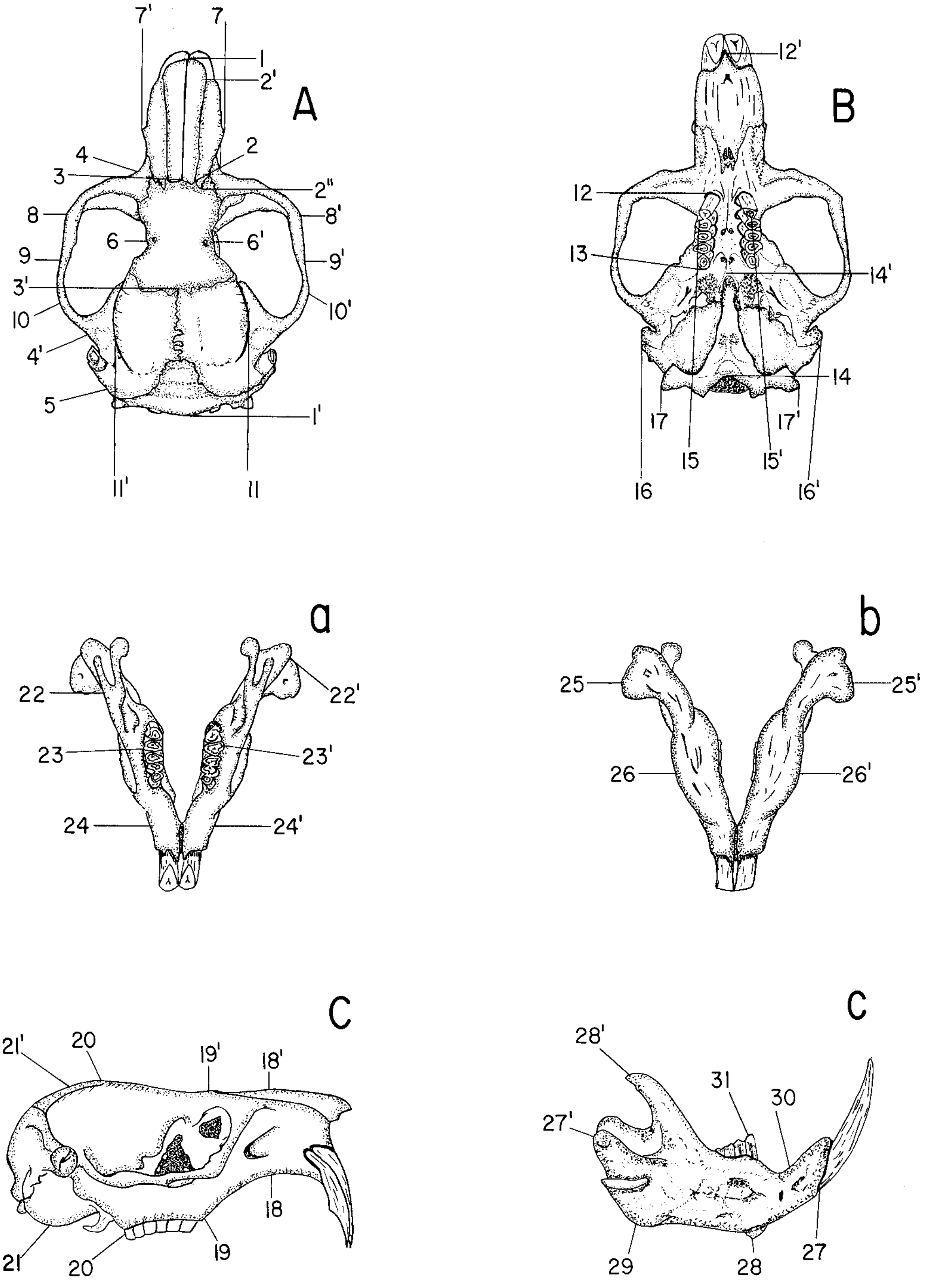


Fig. 1. Cranial measurements (33) taken in 1145 *Thomomys umbrinus* from 72 localities in the Mexican Transvolcanic Belt. **A**, **a**: dorsal view; **B**, **b**: ventral view; **C**, **c**: lateral view. See pp. 13 – 15 for explanations of measurements.

TABLE 1
The 19 Group Localities Sampled in the Mexican Transvolcanic Belt
Abbreviations (Code) refer to the 17 taxa of *Thomomys umbrinus* included in this study.
n = sample size. D.F. = Distrito Federal. See map in figure 2.

Code	Taxon	Group locality	State	n
P	*T. u. pullus*	Pátzcuaro	Michoacán	58
N	*T. umbrinus* ssp.	Cerro San Andrés	Michoacán	27
L	*T. umbrinus* ssp.	Lengua de Vaca	Mexico	25
B	*T. umbrinus* ssp.	Amanalco de Becerra	Michoacán, Mexico	67
C	*T. umbrinus* ssp.	Sierra de las Cruces	Mexico	42
O	*T. u. tolucae*	Volcán Nevado de Toluca	Mexico	102
E	*T. u. peregrinus*	Salazar	Mexico, D.F., Morelos	72
V	*T. u. vulcanius*	Volcán Popocatépetl	Mexico, Puebla	88
M	*T. u. martinensis*	San Martín Texmelucan	Puebla	47
A	*T. u. albigularis*	Sierra de Pachuca, El Chico	Hidalgo, Puebla	82
X	*T. umbrinus* ssp.	Sierra de Tlaxco	Tlaxcala, Puebla	407
I	*T. umbrinus* ssp.	Volcán La Malinche	Tlaxcala, Puebla	92
R	*T. u. orizabae*	Volcán Pico de Orizaba	Puebla	62
S	*T. u. umbrinus*	Boca de Monte	Puebla, Veracruz	5
T	*T. umbrinus* ssp.	Totoltepec	Puebla	5
D	*T. umbrinus* ssp.	La Soledad	Tlaxcala	12
Y	*T. umbrinus* ssp.	Oyameles	Puebla	8

found, Duncan's Test for Multiple Means or Tukey's Test for the Student-Type Range (PROC GLM) were used, respectively (Ott, 1984), in order to determine subgroups among the means.

We considered age variation separately for males and females and, at the beginning, all of the specimens were included. However, since young (age class 1) became separated from the others in 86.65% of all features, we eliminated class 1. Both analyses are presented, but emphasis is given from subadults on (age classes 2–4). Accordingly, for secondary sexual dimorphism, analyses included each age group separately, and the young specimens were excluded.

We ran two-way analysis of variance followed by Duncan's test (PROC GLM) to determine the effect of sex, age, and the interaction between sex and age on the variance in the examined sample (Hollander, 1990; Stangl et al., 1991). In Duncan's tests on sex and age, only the specimens aged 2 and up were considered. Finally, in order to understand the role played by sex, age, and their interaction within total nongeographic variation in *Thomomys umbrinus*, we analyzed the components of the variance (Straney, 1978; Leamy, 1983; Patton and Smith, 1990) using the VARCOMP routine.

GEOGRAPHIC VARIATION

We examined the morphometric similarities among the populations of *Thomomys umbrinus* from the MTB by arranging the sample localities (n = 76) into 17 group localities (GL, table 1, fig. 2). Both nearness and ecological homogeneity were considered in attempting to select groups with no geographic or ecological barriers that would restrict gene flow within each group (Patton and Smith, 1990).

Based on the analysis of intrapopulation variation, we calculated the nature and magnitude of geographic variation of *T. umbrinus* in the MTB separately for both sexes and age classes (2–4).

Statistical programs exclude individuals lacking information in any of the variables; therefore, to include the greatest number of specimens and GLs, a regression analysis (PROC GLM, SAS) was developed to estimate the missing values in individuals. Specimens lacking more than two measurements were excluded from the analysis (n = 30). Likewise, some measurements were eliminated because they were missing in several specimens (BCP, BJT, AWD, GWM, MWD); were too variable (TOL, LVT, HFT, LOE; BOP; and BML); contributed no information

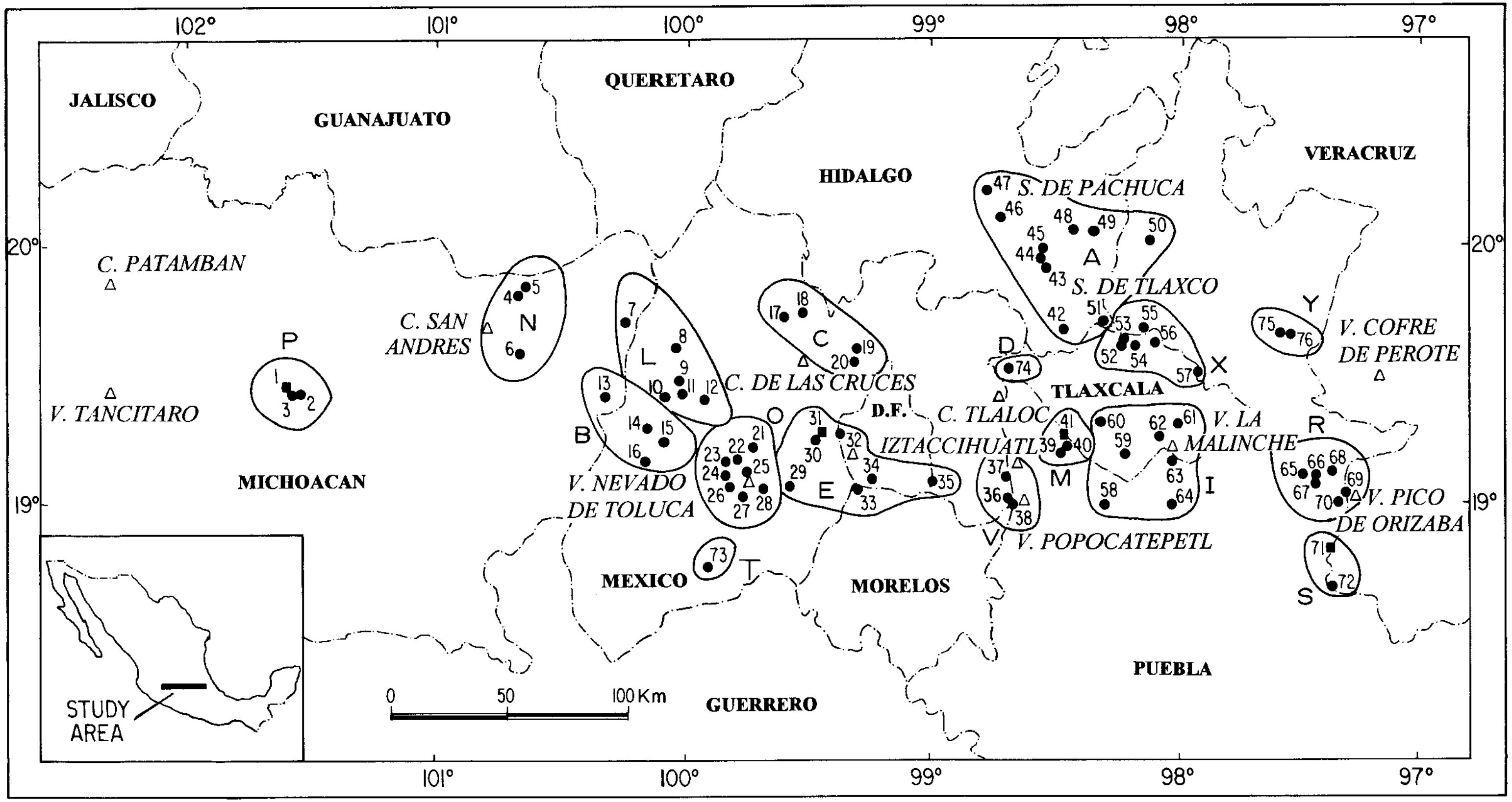


Fig. 2. Group localities (GL's) analyzed in the geographic variation of *Thomomys umbrinus* from the Mexican Transvolcanic Belt. Numbered dots signal sample localities according to specimens examined in text. Circling lines show the group localities according to table 1.

to differentiate among the GLs; or were highly correlated to other variables like MWZ and PWZ (R = 0.8, Castro-Campillo et al., 1993).

Geographic variation was examined by univariate and multivariate statistical analyses. Standard statistics were calculated for each variable with UNIVARIATE (SAS) and then a one-way ANOVA (GLM, SAS) was run to disclose significant ($p < 0.05$) interpopulation differences among means of the GLs. This analysis was completed by Duncan's Test for Multiple Means (SAS) to find population subgroups with no significant differences. The ANOVA was made on the GLs having four or more specimens.

Principal Components Analysis (PCA) with the PRINCOMP (SAS) routine on the measurements of each specimen determined the trends in the variation pattern. Results are summarized in a bidimensional graphic of the first (PC I) and third (PC III) principal components where the distribution of each GL is represented by polygons with their respective centroids. We present PC III instead of PC II in this plot for the sake of clarity, since in the plot of PC I vs PC II, there was an overall massive overlapping of the polygons. We developed another PCA on the population measurements of the GLs and for the tridimensional representation of this analysis, we used the statistical package Numerical Taxonomy System NT-SYS (Rohlf and Kishpaugh, 1972; Rohlf, 1988). A minimum spanning distance tree (MST), calculated from the correlation matrices, was projected onto the first three PCs (Gower and Ross, 1969; Rohlf, 1970, 1973, 1975). In that analysis, as in the rest of the multivariate analyses, all specimens were included.

Cluster analyses were run on the sample means of all the variables in each GL (Sneath and Sokal, 1973), using NT-SYS program. Group populations with a greater phenetic similarity were obtained, using the average taxonomic distance as a similarity measurement and the unweighted pair-group method based on arithmetic averages (UPGMA). We followed this procedure for all age groups with sexes separate, as well as in 12 localities where subadult (2) and adult (3) specimens were collected. The cophenetic coefficient (r) of each phenogram was calculated (Lapointe and Legendre, 1992) and to compare the results, Mantel's tests were developed on the correlation and similarity matrices (Mantel, 1967; Rohlf and Fisher, 1968; Sokal, 1979; Smouse et al., 1986).

Furthermore, a classification discriminant analysis (DISCRIM, SAS) was used to determine the number of specimens correctly assigned according to the acknowledged designation or to the GL of origin (Castro-Campillo et al., 1993). This analysis also determined the degree of overlap among the GLs because of misclassified specimens (Castro-Campillo et al., 1993).

Finally, a brief analysis related pelage coloration to original descriptions (Nelson and Goldman, 1934; Hall and Villa, 1948). For this analysis, only the type specimens and the material deposited at UAMI were reviewed. Pelage shade is described according to Smithe (1974a, 1974b) with the names and color numbers in parentheses after the description.

SPECIMENS EXAMINED

Group localities of previously recognized subspecies and other populations of *Thomomys umbrinus* examined along the MTB are listed from west to east according to table 1 and figure 2. Taxonomic names are followed by the abbreviated (table 1) and the spelled-out name corresponding to the group localities (GLs) mentioned in tables, figures, and text. Next, the total number of specimens examined is indicated in parentheses. Within the sampled localities (SL), the type locality is indicated by an asterisk and if the holotype was examined, its sex, age, catalog number, and the abbreviation for its institutional location are indicated also after the name of the GL. The SLs are preceded by their assigned number according to figure 2 and followed by the number of examined males (♂) and females (♀), and housing museum in parentheses.

Thomomys umbrinus pullus. P = *Pátzcuaro* (45). Michoacán: 2. – 7 km SE Pátzcuaro, 2380 m * (8♀ 5♂ CB); 3. – Los Tanques, 2450 m (21♀ 11♂ UAMI).

Thomomys umbrinus ssp. N = *Cerro de San Andrés* (26). Michoacán: 4. – Laguna Verde, 12.5 km N, 18 km W Cd. Hidalgo, 2790 m (1♀ 1♂ UAMI); 5. – Los Azufres, 2790 m (1♀ UAMI); 5. – Los Azufres, 2850 m (6♀ 5♂ UAMI); 6. – Pucuato, 8 km S, 15 km W, Ciudad Hidalgo, 2400 m (5♀ 7♂ UAMI).

Thomomys umbrinus ssp. L = *Lengua de Vaca* (25). Michoacán: 7. – Cerro Prieto, 8 km S, 3 km W Tlalpujahua, 2780 m (1♀ UAMI). México: 8. – Laguna del Carmen, 2800 m (7♀ 2♂ UAMI); 9. – Cuesta del Carmen, 3 km N, 1 km W, Lengua de Vaca, 2260 m (1♂ CB as *peregrinus*); 10. – 7.5 km S, 2 km E Palizada, 2000 m (1♀ 1♂ UAMI); 11. – 8 km S Lengua de Vaca, 2480 m (6♀ 5♂ UAMI); 12. – 4.5 km S, 10 km W Villa Victoria, 2560 m (1♀ CB).

Thomomys umbrinus ssp. B = *Amanalco de Becerra* (59). Michoacán: 13. – 8 km E Zitácuaro, 2210 m (25♀ 14♂ UAMI); 13. – 9 km E Zitácuaro, 2300 m (2♀ 1♂ UAMI). México: 14. – 12 km NW Amanalco de Becerra, 2720 m (9♀ 1♂ UAMI); 15. – 10 mi N, 6 mi E Valle de Bravo, 7640 ft (2♀ 3♂ KU); 16. – 1.5 mi S Valle de Bravo 6050 ft (7♀ 5♂ KU).

Thomomys umbrinus ssp. C = *Sierra de las Cruces* (42). México: 17. – 2.7 km N, 9 km W Villa del Carbón, 2670 m (1♀ CB as *peregrinus*); 18. – Monte de Peña, 2630 m (21♀ 11♂ UAMI); 19. – 9 km N Jilotzingo, 3260 m (3♀ UAMI); 20. – Jilotzingo, 3260 m (3♀ 3♂ UAMI).

Thomomys umbrinus tolucae. O = *Nevado de Toluca* (101). Holotype: Male, age 4 (55908 USNM).- México: 21. – 3 km SE Zinacantepec, 3000 m (28♀ 15♂ UAMI); 22. – 5 km S, San Juan de las Huertas, 3150 m (2♀ 7♂ CB as *peregrinus*); 23. – Nevado de Toluca, 16 mi SSW Toluca (7♀ 2♂ USNM); 23. – Nevado de Toluca, 16 mi SSW Toluca (1♂ CB); 24. – Nevado de Toluca, 4 mi S Raíces Toluca (3♀ 4♂ USNM); 25. – Nevado de Toluca (NW slope), 11200 ft (5♀ 2♂ KU); 25. – N slope Nevado de Toluca, 9500 ft * (12♀ 3♂ USNM); 26. – La Saavana, 4 km N Raíces, 2500 m (4♀ 1♂ UAMI); 27. – Nevado de Toluca, 6 km S, 5 km W Raíces, 4080 m (4♀ UAMI); 28. – Nevado de Toluca, 13 mi S Toluca (1♂ USNM).

Thomomys umbrinus peregrinus. E = *Salazar* (69). Holotype: Female, age 3 (50130 USNM).- México: 29. – 7.5 km E Tenango de Arista, 2600 m (5♀ 1♂ CB); 30. – 1 mi WSW Salazar, 9500 ft (1♀ 1♂ KU); 30. – 1 mi W Salazar, 9850 ft (3♀ 4♂ KU); 30. – 1 mi W. Salazar, 9800 ft (2♀ KU); 31. – Salazar, 10300 ft * (12♀ 2♂ USNM); 31. – Salazar, 9000 ft (1♀ USNM); 31. – Valle de Toluca, 9000 ft (1♀ USNM); 31. – Salazar, 3050 m (4♀ 2♂ CB); 32. – La Marquesa, 2950 m (9♀ 5♂ CB). Morelos: 33. – 5 km N Tres Cumbres, 10,200 ft (4♀ 8♂ TCWC); 35. – Cicitepec, 15 km S, 5 km E Milpa Alta (1♀ CB). Distrito Federal: 34. – 2 mi SSW Parres, 9800 ft (2♀ 1♂ KU as *peregrinus*).

Thomomys umbrinus vulcanius. V = *Popocatépetl Volcanoe* (88). Holotype: Female, age 2 (51885 USNM).- México: 36. – 86 km SE Mexico City, N slope Mt. Popocatépetl, 13500 ft (8♀ 6♂ TCWC); 36. – Paso de Cortés, 3700 m (2♀ 1♂ CB); 38.- Mt. Popocatépetl, 12900 ft * (1♀ USNM). Puebla: 37. – 6 km N Paso de Cortés, 3830 m (9♀ 6♂ UAMI); 37. – 5 km N Paso de Cortés, 3810 m (8♀ 7♂ UAMI); 37. – 4 km N Paso de Cortés, 3710 m (18♀ 11♂ UAMI); 37. – 2.5 km N Paso de Cortés, 3670 m (2♀ 1♂ UAMI); 38. – 15 km NW San Martin, Río Otalti, 8700 ft (3♀ 5♂ TCWC).

Thomomys umbrinus martinensis. M = *San Martin Texmelucan* (47). Holotype: Female, age 2 (55622 USNM).- Puebla: 39. – San Luis Coyotcingo (through San Pedro Coxtocan Ranch) (1♀ USNM); 40. – Hacienda San Pedro Coxtocan, km 96.5 Pue.-Mex. Hgwy. (18♀ 26♂ USNM); 41. – San Martín (Texmelucan], 7400 ft * (2♀ USNM).

Thomomys umbrinus albigularis. A = *Sierra of Pachuca, El Chico* (81). Holotype: Female, age 2 (5188 USNM).- Hidalgo: 42. – 1 km E Hacienda Tepozán, Municipio de Almoloya, 2700 m (1♂ UAMI); 43. – 8 km E Singuilucan, 2760 m (1♂ UAMI); 44. – Mirasol, 2530 m (3♀ 3♂ UAMI); 45. – Cuatro Palos, 2500 m (35♀ 18♂ UAMI); 46. – Real del Monte, 9500 ft (2♀ 1♂ USNM); 47.- Parque Nacional El Chico, 2860 m (1♀ UAMI); 47. – El Chico, Sierra de Pachuca, 9800 ft * (3♀ USNM); 48. – Tulancingo, Sierra de Pachuca, 8500 ft (1♀ USNM); 49. – 5 mi E Tulancingo, 7400 ft (6♀ 5♂ KU); 51. – 4 km NW El Carmen, Municipio Almoloya, 2680 m (1♀ UAMI). Puebla: 50. – 10 km E, 1 km S Ahuazotepec, 2300 m (1♀ UAMI).

Thomomys umbrinus ssp. X = *Sierra de Tlaxco* (369). Tlaxcala: 52. – Acopinalco del Peñón, 2730 m (3♀ 2♂ UAMI); 52. – Acopinalco del Peñón, 2800 m (1♂ UAMI); 53. – Ejido el Peñón, 2960 m (17♀ 21♂ UAMI); 53. – 1 km E Ejido el Peñón, 2950 m (8♀ 1♂ UAMI); 54. – El Final de la Senda, 2700 m (15♀ 3♂ UAMI); 54. – El Final de la Senda, 2750 m (23♀ 16♂ UAMI); 54. – 1 km S El Final de la Senda, 2700 m (1♀ 1♂ UAMI); 54. – Final de la Senda, límite Puebla-Tlaxcala, 15 km N Tlaxco, 2856m (1♀ 3♂ UAMI); 54. – Límite Puebla-Tlaxcala, 15 km N Tlaxco, 2750 m (6♀ 5♂ UAMI); 54. – Límite Puebla-Tlaxcala, 15 km N Tlaxco, 2750 m (6♀ 2♂ UAMI); 54. – Límite Puebla-Tlaxcala, 15 km N Tlaxco, 2856 m (7♀ 1♂ UAMI); 54. – 15 km N, 3 km E Tlaxco, 2865 m (1♀ UAMI); 54. – 2 km N, 1 km E Tlaxco, 2880 m (5♀ 1♂ UAMI); 54. – 3 km N, 1 km E Tlaxco, 2640 m (1♀ 5♂ UAMI); 54. – 3 km N, 1 km E Tlaxco, 2820 m (87♀ 51♂ UAMI); 54—5 km N, 3 km E Tlaxco, 2600 m (1♀ 1♂ UAMI); 54. – 5 km N, 3 km E Tlaxco, 2920 m (1♀ 1♂ UAMI); 54. – 5 km N, 3 km E Tlaxco, 2960 m (2♀ 1♂ UAMI); 54. – 6 km N, 2 km E Tlaxco, 2770 m (2♀ 2♂ UAMI); 54. – 8 km N Tlaxco, 2820 m (1♀ UAMI); 56. – Paso Ancho, 12.5 km N, 6 km E Tlaxco, 2620 m (3♀ 2♂ UAMI); 57. – Villarreal, 3000 m (26♀ 14♂ UAMI). Puebla: 55. – Ciénega Larga, 12 km S, 5 km W Chignahupan, 2640 m (15♀ 12♂ UAMI); 55. – Agua Santa, 13.5 km S, 5 km W Chignahuapan, 2740 m (1♀ UAMI).

Thomomys umbrinus ssp. I = *Monte La Malinche* (90). Tlaxcala: 58. – La Junta (1♂ USNM); 59. – Cd. Industrial Xicoténcatl, 2510 m (1♀ 1♂ UAMI); 60. – 1 km S Sta. Cruz Techachalco, 2080 m (1♀ UAMI); 61. – 7 km S, 11 km E Apizaco, 2600 m (2♀ UAMI); 61. – 8 km S, 8 km E Apizaco, 2600 m (6♀ 4♂ UAMI); 61. – 8.5 km S, 9.5 km E Apizaco, 2620 m (7♀ 1♂ UAMI); 61. – 8 km S, 11.5 km E Apizaco, 2600 m (5♀ 8♂ UAMI); 62. – Monte La Malinche, 2.5 km S, 11 km W Huamantla, 3000 m (38♀ 13♂ UAMI); 63. – S slope Malinche volcano, 3800 m (1♀ USNM); 64. – San Felipe Tenextepec (1♀ USNM).

Thomomys umbrinus orizabae. R = *Pico de Orizaba Volcanoe* (72). Holotype: Female, age 3 (53616 USNM).- Puebla: 65. – Miguel Hidalgo y Costilla, 3260 m (24♀ 20♂ UAMI); 66. – 16 km NE San Andrés, W slope Orizaba, 11,000 ft (1♀ TCWC); 66. – 12 km NNE San Andrés, NW slope Mt. Orizaba, 10,000 ft (2♀ TCWC); 66. – 12 km NNE San Andrés, W slope Orizaba, 10,000 ft (2♀ TCWC); 67. – 6.5 km S, 10.5 km E Tlalchichuca 3100 m (1♂ CB); 67. – 6.5 km S, 10 km E Tlalchichuca, 3100 m (1♀ 1♂ CB); 68. – 10 km N, 12.4, E Cd. Serdán, 3340 m (3♀ 1♂ CB); 69. – Mt. Orizaba, 9500 ft * (10♀ 5♂ USNM); 70. – 2.5 km N, 15.5 km E Ciudad Serdán, 3280 m (1♀ CB).

Thomomys umbrinus umbrinus. S = *Boca de Monte* (9). Veracruz: 71. – Boca del Monte, 7800 ft * (4♀ 4♂ USNM); 72. – 2 km N, Los Jacales, 4500 ft (1♀ KU)

Thomomys umbrinus ssp. T = *Totoltepec* (5). México: 73. – 4.6 km SE Totoltepec, 2540 m (2♀ 3♂ UAMI).

Thomomys umbrinus ssp. D = *La Soledad* (12). Tlaxcala: 74. – 3 km S La Soledad 2900 m (10♀ 2♂ UAMI).

Thomomys umbrinus ssp. Y = *Oyameles* (5). Puebla: 75. – 10 Km E Oyameles, 2500 m (1♀ 2♂ UAMI); 75. – 7 km E Oyameles, 2550 m (1♀ 3♂ UAMI); 76. – 4.2 km W Oyameles (1♀ CB).

RESULTS

NONGEOGRAPHIC VARIATION

INDIVIDUAL MORPHOMETRIC VARIATION

In general, CVs of the external measurements averaged greater for all ages in both sexes, followed by the mandible measurements and then by those of the braincase and rostrum (table 2). CVs ranged between 1.9 for LBC in old females (♀4) and 14.5 for LVT in young males (♂2). Individual variation differed according to sex with females showing less variation than males, except for the oldest females (♀4) whose variation was slightly greater than in males of the same age (♂4). Indeed, old females (♀4) exhibited a

TABLE 2

Average Coefficients of Variation (CVs) in a Sample of 356 Specimens of *Thomomys umbrinus* from Sierra de Tlaxco in the State of Tlaxcala

CVs were calculated in 4 external, 22 cranial, and 11 jaw measurements by sex and age category (juvenile = 1; subadult = 2; adult = 3; old = 4). Sample sizes (n) are shown for each age group; mean and total are given for each sex.

Age	External	Cranial	Jaw	n
		Females		
1	7.4	4.4	5.0	22
2	8.1	5.0	5.7	104
3	8.2	4.2	4.9	80
4	7.7	5.3	6.7	8
Mean (Total)	7.8	4.7	5.6	(214)
		Males		
1	10.1	5.4	8.7	19
2	8.4	5.0	7.1	42
3	7.6	4.1	4.0	57
4	8.3	4.1	6.5	24
Mean (Total)	8.6	4.6	6.6	(142)

greater individual variation in all of their measurements than females of the other age groups (♀2–3). Among the latter, subadult females (♀2), revealed a greater overall variation than the young (♀1) and the adult (♀3) females. Males differed in that the young (♂1) were more variable in all measurements, subadult (♂2) and old (♂4) males showed an overall comparable variation, and adult (♂3) males showed a smaller variation.

In external measurements (table 2), young females (♀1) showed less variation, followed by old females (♀4), subadults (♀2), and adults (♀3). In skull characters, adult females (♀3) showed less variation followed by young (♀1), subadult (♀2), and old (♀4) females. Adult males (♂3) showed less variation in external and mandibular measurements than old (♂4), subadult (♂2), and young (♂1) males, respectively. However, they showed the same lower variation in measurements of the braincase as the old males (♂4) as compared to subadult (♂2) and young (♂1) males, respectively.

In both sexes and in all ages, the most variable external characters were LVT (CV = 6.1–4.6) and LOE (CV = 8.0–12.2), while HFT (CV = 5.7–8.0) and TOL (CV = 3.7–8.8) were the least variable. For the skull, BOP (CV = 6.8–9.1), LMX (CV = 5.0–6.3), and LNA (CV = 5.3–6.9) reach a greater variation between the females of all ages. LNA (CV = 7.4,7.5) together with WRO (CV = 7.7, 5.9) and HMC (CV = 7.4, 5.8) were also the most variable characters in both young (♂1) and subadult males (♂2). Whereas in females, the skull measurements with smaller variation were LBC (CV = 1.9–2.9), TLS (CV = 2.0–3.2), and SBP (CV = 2.5–4.1), in males it was BAB (CV = 2.5–3.7). For the jaw, measurements with greater variation in females were AWD (CV = 7.6–9.2), DHI (CV = 5.2–8.6), and BJT (CV = 5.5–7.4), while in males it was also AWD (CV = 7.0–12.1), besides AHM (CV = 9.4–10.0), and BML (CV = 7.7–11.9). Mensurable characters with smaller CVs were BCP (CV = 2.8–7.7) and GLD (CV = 2.9–6.2) in both sexes; although, young males (♂1) showed a greater variation.

ONTOGENETIC VARIATION

Table 3 shows the ontogenetic variation among subadult (age 2), adult (age 3), and old specimens (age 4) according to a single ANOVA. Results show that the age categories separated in a high proportion of variables. Differences in patterns are also shown by the sexes: in males, fewer variables showed no differences between ages (LVT, LOE, and BAM) than in females (HFT, LVT, ICO, LPF, BAM, BOP, HBP, and BML). Especially, old females (age 4) segregated more from other females than males of the same age with respect to other males (table 3).

In the analyses in which ages 1–4 were considered collectively, variables with no differences among females were LVT, HFT, and ICO; only ICO and BOP showed no differences among males of different ages. Among younger specimens (age 1), ICO differed more than that of the other ages. Young specimens segregated in almost every variable, regardless of their sex, and, therefore, they were excluded from all of the later analyses. In general, in both analyses, variables showing discontinuity between age groups,

TABLE 3

Effect of Age on 37 Variables (Var) in a Sample of 306 Specimens of *Thomomys umbrinus* from Sierra de Tlaxco in the State of Tlaxcala, According to an Analysis of Variance (F)

Within Duncan's test, a hyphen indicates no differences between the means of the involved age groups (subadults = 2; adults = 3; old = 4), and a comma indicates differences. All tests were significant ($0.0001 \leqslant p \leqslant 0.05$) unless marked by with asterisk. For definitions of variables, see the Measurements section in the Introduction.

	Males		Females			Males		Females	
Var	F	Duncan	F	Duncan	Var	F	Duncan	F	Duncan
TOL	33.0	4, 3, 2	19.3	4, 3, 2	LVT	3.6	4-3, 3-2	*1.6	4-3-2
HFT	8.0	4-3, 2	4.1	4-3, 3-2	LOE	3.5	4-3, 3-2	4.3	4-3, 2
GLS	82.1	4, 3, 2	76.9	4, 3, 2	LNA	46.0	4, 3, 2	55.4	4, 3, 2
LMX	55.6	4, 3, 2	40.1	4, 3, 2	LFO	12.7	4-3, 2	9.6	4, 3-2
LZA	67.5	4, 3, 2	54.0	4, 3, 2	LBC	70.5	4, 3, 2	53.9	4, 3, 2
WRO	48.0	4, 3, 2	41.7	4, 3, 2	ICO	5.9	4, 3-2	*1.6	4-3-2
AZB	100.8	4, 3, 2	56.8	4, 3, 2	MZB	97.7	4, 3, 2	49.5	4, 3, 2
PZB	114.1	4, 3, 2	49.7	4, 3, 2	SBP	8.5	4-3, 2	14.7	4, 3, 2
LDI	105.6	4, 3, 2	66.1	4, 3, 2	LMT	7.4	4, 3-2	13.3	4, 3, 2
LPF	31.6	4-3, 2	6.7	4-3, 3-2	BAM	8.3	4-3, 2	4.6	4-3, 3-2
BOP	5.2	4-3, 2	3.1	4-3, 3-2	BAB	67.6	4, 3, 2	39.4	4, 3, 2
HRO	38.5	4, 3, 2	26.2	4, 3, 2	HMC	101.5	4, 3, 2	79.1	4, 3, 2
MHS	57.0	4, 3, 2	62.7	4, 3, 2	HBP	7.6	4-3, 2	5.1	4-3, 3-2
BCP	7.1	4-3, 2	18.3	4-3, 2	BJT	*2.7	4-3, 3-2	14.0	4, 3-2
AWD	23.3	4, 3, 2	19.2	4, 3, 2	GWM	18.9	4, 3, 2	68.6	4, 3, 2
MWD	6.9	4-3, 2	28.2	4, 3, 2	GLD	69.5	4, 3, 2	68.0	4, 3, 2
LCP	44.7	4, 3, 2	49.0	4, 3, 2	BML	10.0	4-3, 2	*1.5	4-3-2
DHI	31.8	4, 3, 2	41.0	4, 3, 2	AHM	8.2	4, 3, 2	52.3	4, 3, 2
PHM	69.9	4, 3, 2	53.1	4, 3, 2					

are related to body length and to the length and width of the rostrum and mandible.

SECONDARY SEXUAL DIMORPHISM

In *Thomomys umbrinus* (table 4), significant sexual dimorphism ($p < 0.05$) was more evident among adult (83.8% of the variables) and old specimens (73% of the variables) than among the subadults (27% of the variables). Except for ICO, where subadult females surpassed males of the same group, males exceeded females in all other characters with significant sexual dimorphism.

Males were also larger than females in several variables with no significant sexual dimorphism (old specimens = 35.1% of variables; adult specimens = 13.5%, and subadult specimens = 27%). There were only six measurements where females were significantly larger than males of the corresponding age group: subadult females were larger in BOP, MWD, BAM, BJT, and AHM; adult females in BOP; and old females in BML.

COMBINED EFFECT OF AGE AND SEXUAL DIMORPHISM

Analyses of the combined effect of age and sexual variation supported previous results (table 5). Age groups were separated in every jaw (11 variables), 20 cranial, and two external measurements, allowing the differentiation among the three considered ages. Exceptions were LVT, with no differences between adult and subadult specimens; LOE with no differences between old and adult specimens; ICO with nonsignificant differences among the age groups, although subadults were broader than the other groups; and BOP which showed no differences between old and adult individuals and between adult and subadults.

Sexual dimorphism was also present in almost every variable (35 out of 37), except for ICO and BOP where females were nonsignificantly larger than males (table 5). Interaction between age and sexual dimorphism was positive in one-third of all characters (32%), including one body measure-

TABLE 4

Sexual Dimorphism in 306 Specimens of *Thomomys umbrinus* from Sierra de Tlaxco in the State of Tlaxcala

The ANOVA was performed on 37 variables (Var) using sex and age groups. F values (F) and Tukey's tests (Tu) are shown by age group (subadult = 2, n = 141; adult = 3, n = 133; old = 4, n = 32). Within the latter, > indicates that males were significantly ($0.0001 \leqslant p \leqslant 0.05$) larger than females; ∧ indicates that males were nonsignificantly larger than females; < indicates that females were significantly larger than males; and ∨ indicates that females were nonsignificantly larger than males.

	Age group							Age group					
	2		3		4			2		3		4	
Var	F	Tu	F	Tu	F	Tu	Var	F	Tu	F	Tu	F	Tu
TOL	2.7	∧	33.3	>	14.0	>	LVT	0.7	∧	6.9	>	1.7	∧
HFT	3.0	∧	36.1	>	12.0	>	LOE	11.9	>	10.7	>	3.3	∧
GLS	7.3	>	120.6	>	17.0	>	LNA	3.4	∧	44.2	>	16.4	>
LMX	4.6	>	52.2	>	16.2	>	LFO	0.9	∧	14.7	>	3.0	∧
LZA	1.0	∧	57.0	>	2.9	∧	LBC	6.5	>	96.2	>	7.9	>
WRO	3.6	∧	51.1	>	15.1	>	ICO	4.3	<	6.2	>	3.0	∧
AZB	17.7	>	167.6	>	22.1	>	MZB	21.5	>	147.5	>	17.8	>
PZB	21.9	>	141.8	>	12.8	>	SBP	0.0	∧	3.0	∧	2.0	∧
LDI	9.4	>	169.2	>	9.0	>	LMT	0.1	∧	1.6	∧	4.1	>
LPF	3.2	∧	25.8	>	0.5	∧	BAM	0.0	∨	2.5	∧	1.0	∧
BOP	0.8	∨	0.3	∨	1.6	∧	BAB	6.5	>	86.5	>	16.0	>
HRO	1.0	∧	15.4	>	3.0	∧	HMC	8.3	>	89.7	>	9.5	>
MHS	1.3	∧	40.2	>	15.3	>	HBP	2.9	∧	12.5	>	4.5	>
BCP	3.8	∧	10.4	>	12.7	>	BJT	1.1	∨	0.0	∧	4.9	>
AWD	2.8	∧	26.4	>	10.3	>	GWM	1.9	∧	18.1	>	19.6	>
MWD	0.1	∨	2.7	∧	11.0	>	GLD	3.1	∧	69.4	>	5.2	>
LCP	2.4	∧	37.0	>	9.7	>	BML	0.6	∧	11.9	>	0.1	∨
DHI	0.7	∧	49.6	>	5.0	>	AMH	0.0	∨	4.5	>	8.8	>
PHM	2.8	∧	69.0	>	8.4	>							

ment (LOE), nine cranial measurements (TLS, LZA, LBC, ICO, PZB, LDI, LPF, BAB, and HMC), and three jaw measurements (GLD, DHI, PHM).

Finally, in the analysis of the variance components where only age, sexual dimorphism, and their interaction were considered, almost half of variation was due to these factors (46.91%). Therefore, 25.94% of variation is due to age effect, 19.42% to secondary sexual dimorphism, and 1.55% to the interaction between them. The rest of variation, not specified as a variable and included within the standard error (53.09%), might be due to other factors such as fossorial niche, type of soil, food habits, etc.

GEOGRAPHIC VARIATION

ANALYSES OF VARIANCE

F statistics and Duncan's Test for Multiple Means are available upon request. In general, results of these analyses demonstrated the absence of an overall pattern of variation related to the geographic distribution of the samples in all age classes of both sexes along the MTB (table 6). On the contrary, with the exception of *Thomomys u. pullus*, the general pattern seemed to be that of morphometric similarity among the studied populations regardless of their origin (table 6).

Indeed, every analysis was significant ($p < 0.05$) for the majority of the 24 variables examined and F ranged between 0.94 (HRO) and 14.58 (DHI), both for the male subadults. Duncan's tests showed a highly heterogeneous series among the group locality (GL) subgroups that are formed and varied from one sex to the other, from one age to another and within a single age and sex.

Although the results pointed out differences between the extreme GLs (with greater and lesser magnitude in one variable), in general, the intermediate GLs formed a *con-*

TABLE 5

Sexual Dimorphism (S), Effect of Age (A), and Interaction Between These Two Factors (SA) in 306 Specimens of *Thomomys umbrinus* from Sierra de Tlaxco in the State of Tlaxcala

Analyses were performed on 37 variables (Var) obtained from 141 subadult (age group 2), 133 adult (age group 3), and 32 old (age group 4) specimens. F values (F) and Duncan's tests for Multiple Means (Duncan) are shown. Unless marked by an asterisk, analyses were significant ($0.0001 \leq p \leq 0.05$). To = F value for the whole analysis. See tables 3 and 4 for notation.

	F				Duncan			F				Duncan	
Var	To	S	A	SA	S	A	Var	To	S	A	SA	S	A
TOL	37.7	94.8	46.3	*0.5	>	4, 3, 2	LVT	5.4	16.2	4.9	*0.5	>	4, 3-2
HFT	19.1	70.5	11.1	*1.4	>	4, 3, 2	LOE	8.6	27.2	3.7	4.2	>	4-3, 2
GLS	11.3	244.5	161.3	4.7	>	4, 3, 2	LNA	68.9	138.3	102.0	*1.1	>	4, 3, 2
LMX	66.9	145.2	93.7	*0.9	>	4, 3, 2	LFO	16.5	36.1	22.4	*0.7	>	4, 3, 2
LZA	73.5	114.3	119.6	7.0	>	4, 3, 2	LBC	87.2	176.6	123.1	6.5	>	4, 3, 2
WRO	65.8	144.0	89.6	*2.9	>	4, 3, 2	ICO	3.4	*3.2	*0.8	6.1	v	2-3-4
AZB	110.0	253.1	145.8	*2.6	>	4, 3, 2	MZB	101.5	230.2	136.0	*2.7	>	4, 3, 2
PZB	105.3	228.0	144.9	4.5	>	4, 3, 2	SBP	12.5	16.1	22.9	*0.2	>	4, 3, 2
LDI	118.0	236.2	168.6	8.3	>	4, 3, 2	LMT	11.6	17.2	20.3	*0.3	>	4, 3, 2
LPF	22.5	46.2	28.6	4.5	>	4, 3, 2	BAM	6.2	9.5	10.4	*0.2	>	4, 3, 2
BOP	3.0	*0.2	7.1	*0.3	v	4-3, 3-2	BAB	80.2	191.4	101.1	3.7	>	4, 3, 2
HRO	35.9	52.2	62.5	*1.1	>	4, 3, 2	HMC	114.2	198.8	180.9	5.1	>	4, 3, 2
MHS	75.0	134.5	119.7	*0.6	>	4, 3, 2	HBP	12.3	34.9	12.9	*0.4	>	4, 3, 2
BCP	18.3	46.5	23.5	*0.6	>	4, 3, 2	BJT	8.1	6.8	14.3	*2.5	>	4, 3, 2
AWD	32.7	77.1	42.4	*0.6	>	4, 3, 2	GWM	45.6	84.7	71.7	*0.0	>	4, 3, 2
MWD	18.3	26.4	31.1	*1.5	>	4, 3, 2	GLD	85.8	140.3	140.1	4.4	>	4, 3, 2
LCP	60.2	108.4	95.2	*1.1	>	4, 3, 2	BML	5.9	9.2	7.6	*2.5	>	4, 3, 2
DHI	49.2	95.1	70.9	4.5	>	4, 3, 2	AMH	22.0	30.9	38.8	*0.9	>	4, 3, 2
PHM	78.6	143.5	121.1	3.6	>	4, 3, 2							

tinuum between the extremes. In fact, there were several measurements in which there were no differences among GLs: LPF and BAM in adult females; AZB and MHS in old females; LNA, LZA, and LBC in subadult males; TLS, LNA, LZA, ICO, LPF, MHS, and AHM in adult males.

In contrast to the unclear general pattern, some individual groups from some sampled localities consistently segregated from those in other GLs for several variables. In GL P (*T. u. pullus*), subadult females segregated from other GLs for its small size in TLS, AZB, BAM, BAB, MHS, HMC and subadult males separated for their smaller size in BAM and BAB. In GL I (*T. umbrinus* ssp. from La Malinche Volcano), subadult females segregated according to larger size in AHM and old females for larger size in LBC, HRO, GLD, and DHI. In GL V (*T. u. vulcanius*), adult females segregated according to larger size in SBP, old females in DHI (following GL MM), and old males in BAB. In GL R (*T. u. orizabae*) adult males were smaller-sized in LDI. In GL M (*T. u. martinensis*) old males were larger-sized in LCP. Finally, in GL N (*T. umbrinus* ssp. of the Sierra de San Andres) old males were larger-sized in LZA, HMC, and GLD.

Principal Components Analysis and Minimum Spanning Tree

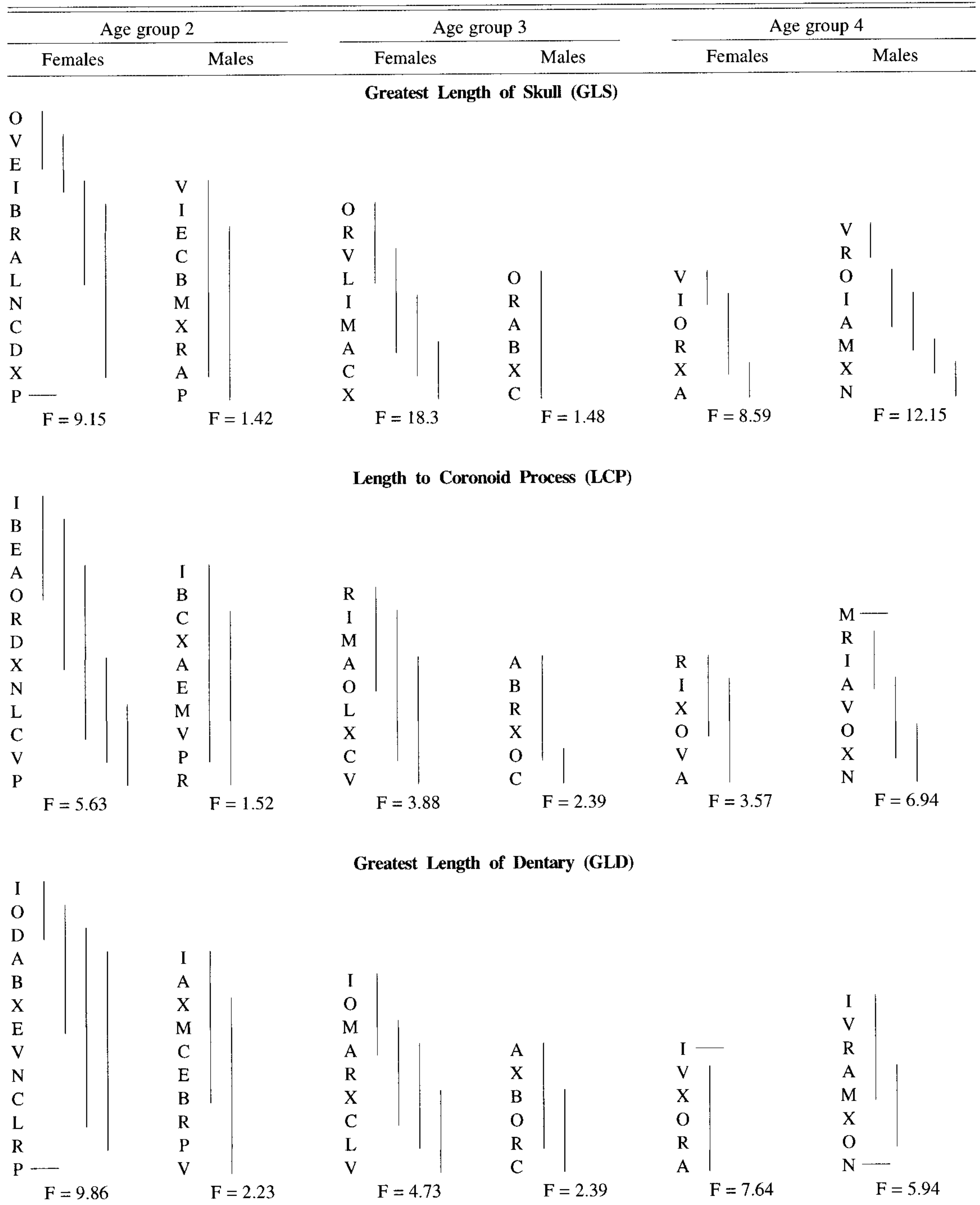
Except for the GL P representing *T. u. pullus* (fig. 3), all GLs overlapped broadly in multispace (figs. 3, 4). Some of the geographically nearest GLs tended to group together (i.e., GLs A and X); however, this is not a rule in every analysis (i.e., minimum spanning trees, fig. 4). Moreover, no consistent geographic pattern related to origin of samples was observed among the GLs groupings according to age or sex (figs. 3, 4).

Distribution patterns of the GLs in multispace were similar between the PCA carried out on the individuals (fig. 3) and the PCA carried out on the sample means of the GLs

TABLE 6

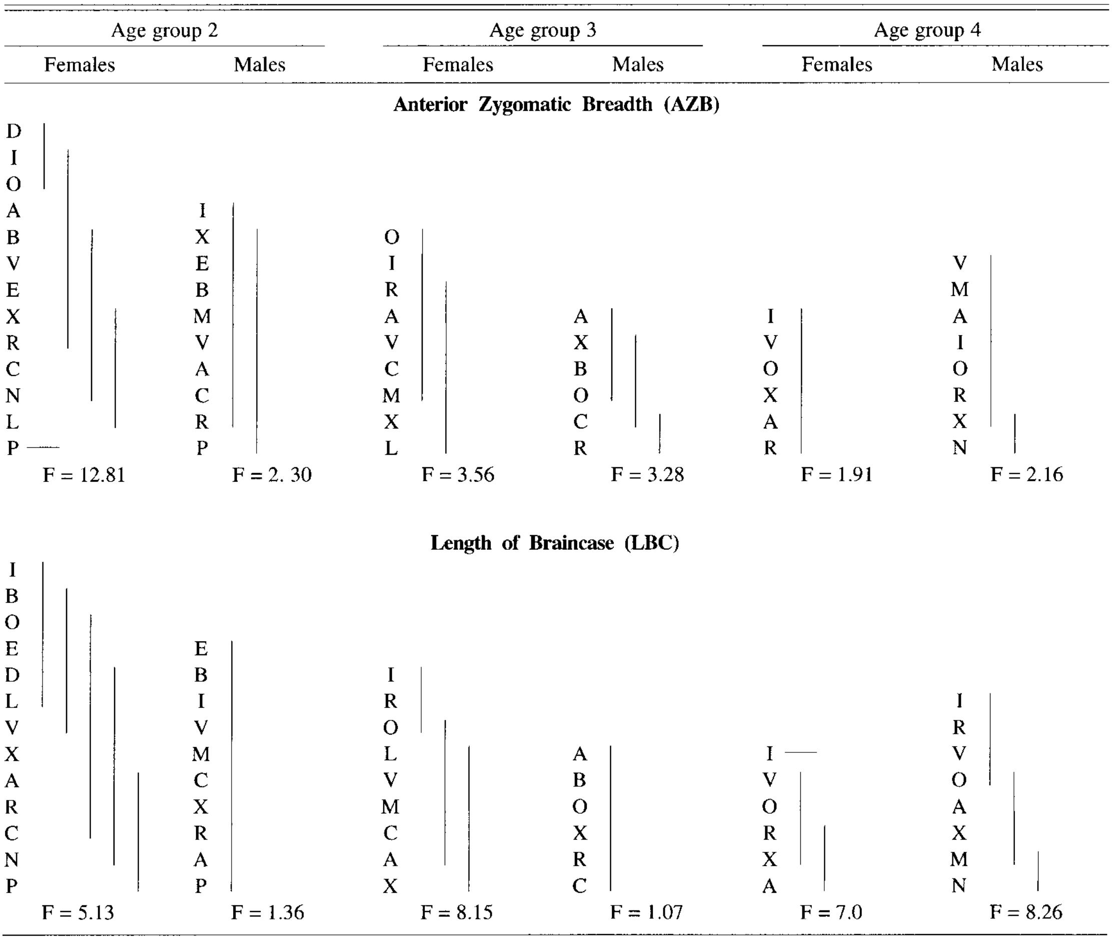
Studied Populations of *Thomomys umbrinus* Along the Mexican Transvolcanic Belt Grouped by Age Category According to Selected Variables in a Multiple Analysis of Variance

Mean size of variables decreases from the top to the bottom. In the Duncan analysis, vertical lines indicate absence of significant differences ($p \leq 0.05$) among populations and horizontal lines indicate significant segregation from the other populations. See table 1 for locality names.



	Age group 2		Age group 3		Age group 4	
	Females	Males	Females	Males	Females	Males
Greatest Length of Skull (GLS)	O V E I B R A L N C D X P —	V I E C B M X R A P	O R V L I M A C X	O R A B X C	V I O R X A	V R O I A M X N
	F = 9.15	F = 1.42	F = 18.3	F = 1.48	F = 8.59	F = 12.15
Length to Coronoid Process (LCP)	I B E A O R D X N L C V P	I B C X A E M V P R	R I M A O L X C V	A B R X O C	R I X O V A	M — R I A V O X N
	F = 5.63	F = 1.52	F = 3.88	F = 2.39	F = 3.57	F = 6.94
Greatest Length of Dentary (GLD)	I O D A B X E V N C L R P —	I A X M C E B R P V	I O M A R X C L V	A X B O R C	I — V X O R A	I V R A M X O N —
	F = 9.86	F = 2.23	F = 4.73	F = 2.39	F = 7.64	F = 5.94

TABLE 6
(Continued)



Age group 2		Age group 3		Age group 4	
Females	Males	Females	Males	Females	Males
Anterior Zygomatic Breadth (AZB)					
D					
I					
O					
A	I				
B	X	O			
V	E	I			V
E	B	R			M
X	M	A	A	I	A
R	V	V	X	V	I
C	A	C	B	O	O
N	C	M	O	X	R
L	R	X	C	A	X
P	P	L	R	R	N
F = 12.81	F = 2. 30	F = 3.56	F = 3.28	F = 1.91	F = 2.16
Length of Braincase (LBC)					
I					
B					
O					
E	E				
D	B	I			
L	I	R			I
V	V	O			R
X	M	L	A	I	V
A	C	V	B	V	O
R	X	M	O	O	A
C	R	C	X	R	X
N	A	A	R	X	M
P	P	X	C	A	N
F = 5.13	F = 1.36	F = 8.15	F = 1.07	F = 7.0	F = 8.26

(fig. 4). However, both analyses differed (table 7) in the most important variables for PC I–III, the percentage of variation explained by PC I–III, and the relation of PC-I to either size or shape.

In the PCA on individuals (table 7), 65.7% of variation was explained by the first three PCs. The highest amount of variation explained was reached in the analysis for subadult males (72.3%) and the lower in both adult males and females, 58% and 58.8%, respectively (fig. 3). PC I explained more than 50% of the total variation, except in both adult specimens (males, 40%; females, 42.7%). P II explained from 7.2% in subadult males to 11.1% in old females, and PC III explained from 4.9% in old males to 8.5% in adult males.

All coefficients had positive sign in PC I, regardless of sex or age (fig. 3, table 7); therefore, in such analyses PC I constituted a component related to the size of the individuals (Pimentel, 1979). Coefficients for PC II and PC III had different sign in all PCAs; therefore these components are related to shape (Pimentel, 1979). According to their coefficients, the first five most important cranial measurements for PC I were TSL, LCP, GDL, LBC, and AZB; for PC II were LCP, LFO, BAB, TSL, and GDL; and for PC III were LCP, LFO, BAB, LNA, and HBP.

In the PCA on the GL means (fig. 4, table

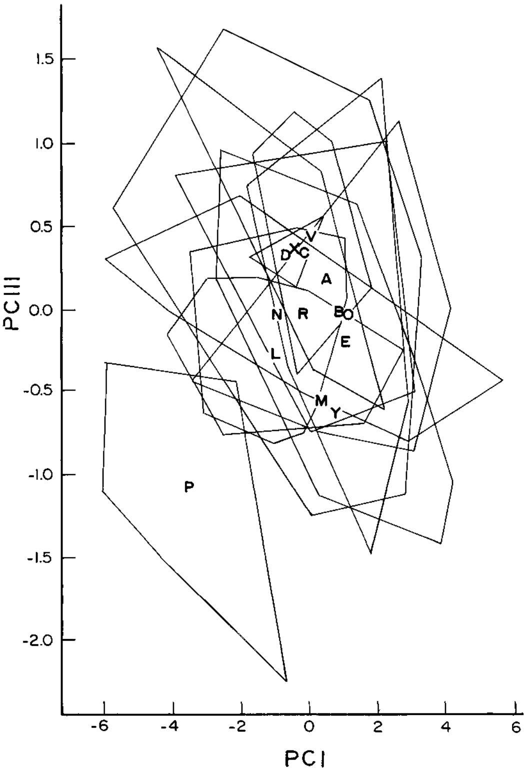


Fig. 3. Bidimensional distribution of subadult females in the principal components (PC) III and I. *Thomomys umbrinus pullus* (P) is separated from other examined populations along the Mexican Transvolcanic Belt by both its small size and cranial morphology. Letters indicate the centroids of each examined sample as mentioned on table 1. The analysis was made on the individuals.

7), 79% of variation was explained by the first three PCs. In this analysis (fig. 4), the highest amount of variation was explained in the analysis for adult males (89.4%) and the lowest in that for females of the same age (69.5%). PC I explained from 36.9% (adult females) to 74.1% (adult males) of the total variation among samples; PC II from 9.4% (adult males) to 33.9% (subadult females); and PC III from 4.9% (old males) to 15.4% (old females).

Since all coefficients had positive signs in PC I for old males (fig. 4, table 7), this function represents size tendencies among GLs (Pimentel, 1979). Coefficients in the other analyses had different signs for all PCs (fig. 4, table 7); therefore, these components are related to shape (Pimentel, 1979). In PC I, the most important measurements for old males were TLS, GDL, LCP, LBC, and AZB, while for the other specimens they were TLS, LCP, PHM, GDL, AZB. In PC II the most important measurements were TLS, LCP, LNA, GDL; LFO, and BAB, and in PC III LFO, LMX, PHM, GDL, and LCP.

Comparison of patterns in plots of figure 4 revealed no consistent pattern among the outstanding variables in relation to sex, age group, or GL, because they were not always the same or in the same sequence (table 7). However, it is evident that the coefficients of the five most important variables surpassed the others considerably in every case and that there were variables with almost no importance at all (table 7).

The majority of the coefficients in the PCA on individuals, as in the PCA on the means, showed a positive sign that indicates an increase in the dimensions of these variables among the studied populations (table 7). On the other hand, the variables that showed a negative coefficient can be interpreted as having a decrease in magnitude among the populations (Pimentel, 1979). Such variables were LFO in subadult females; BAB and HBP in adult females; AZB and SBP in old females; LNA, LMX, LFO, WRO, and LPF in subadult males; and TLS, LBC, WRO, AZB, LPF, BAM, BAB, HRO, HMC, GLD, and LCP in adult males (table 7).

It can be pointed out that all of the variables of the first analysis were included in those outstanding in the second analysis, except for SBP, LZA, and HBP (table 7). Regarding size, these variables (especially TLS, LFO, LCP, and GLD) allowed the distinction of the *T. u. pullus* individuals from the rest due to their shorter dimensions. In shape, this subspecies was also distinguished from other examined *T. umbrinus* by a lesser expansion of the zygomatic arches (AZB, MZB, PZB) and by a general smoother appearance of the skull.

According to the minimum spanning tree (MST) projected onto the PCA (fig. 4), some populations showed morphophenetic relations with more than one population (GLs X, O, B, A, R, N, M, L, C, I), while others linked with only one (P, T, D, E, S, Y). Phenetic distances were shorter between some

TABLE 7

Percentage of Variation Explained by the First Three Principal Components (% PC I–III) and Their Coefficients for 24 Cranial Variables (Var) Measured in *Thomomys umbrinus* from 17 Populations Along the Mexican Transvolcanic Belt

A first principal components analysis (PCA) was computed using all specimens (Individuals) and a second PCA with the population averages (Means). Analyses were developed by separated sexes and age groups. The total percentage of variation explained by PC I–III (% PC) is given for each analysis.

	Individuals, Females								
% Total:	Age group 2 = 65.7%			Age group 3 = 58.8%			Age group 4 = 68.8%		
Var	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
GLS	0.47	−0.45	0.15	0.55	−0.44	0.17	0.45	−0.38	−0.06
LNA	0.18	−0.29	−0.27	0.23	−0.35	−0.28	0.21	−0.09	0.02
LMX	0.16	−0.22	−0.24	0.20	−0.22	−0.15	0.20	−0.24	0.10
LFO	0.12	−0.48	0.44	0.16	−0.17	0.43	0.16	−0.48	0.54
LZA	0.21	−0.02	−0.11	0.19	0.15	0.15	0.25	0.17	0.16
LBC	0.25	−0.12	0.02	0.28	0.11	0.20	0.26	0.14	−0.15
WRO	0.09	−0.06	0.05	0.13	0.02	-0.01	0.11	−0.07	−0.02
ICO	0.04	0.00	0.08	0.03	0.10	0.10	0.05	−0.13	0.18
AZB	0.33	0.33	0.21	0.25	0.10	−0.14	0.22	0.10	0.14
SBP	0.06	0.06	0.14	0.08	0.11	0.22	0.15	−0.11	0.29
LDI	0.23	−0.03	−0.15	0.21	−0.20	−0.11	0.24	−0.09	0.05
LMT	0.08	−0.00	−0.02	0.09	0.10	0.01	0.10	−0.03	0.03
LPF	0.07	0.04	−0.00	0.10	0.04	0.03	0.07	0.03	0.04
BAM	0.09	0.13	0.16	0.03	0.06	−0.07	0.06	−0.10	0.01
BAB	0.22	0.38	0.41	0.14	0.31	0.55	0.23	−0.13	0.33
HRO	0.08	−0.02	0.03	0.11	0.07	0.00	0.12	0.07	0.07
HMC	0.19	−0.01	−0.08	0.21	0.03	−0.06	0.21	−0.02	−0.09
MHS	0.14	0.09	0.12	0.12	0.03	−0.09	0.14	0.10	0.05
HBP	0.09	0.13	0.15	0.07	0.08	0.11	0.08	0.19	0.07
GLD	0.32	0.13	−0.00	0.27	0.21	−0.09	0.33	0.17	0.22
LCP	0.35	0.21	−0.55	0.31	0.35	−0.36	0.24	0.42	−0.54
DHI	0.05	−0.00	−0.04	0.08	0.08	−0.03	0.10	0.01	0.10
AHM	0.12	0.08	−0.07	0.11	0.16	−0.09	0.18	0.12	0.12
PHM	0.20	0.20	−0.10	0.16	0.41	−0.21	0.21	0.39	0.07
% PC	51.6	8.4	5.7	42.7	9.1	7.0	50.0	11.0	7.8

	Individuals, Males								
% Total:	Age group 2 = 72.3%			Age group 3 = 58.0%			Age group 4 = 70.3%		
Var	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
GLS	0.41	−0.28	0.36	0.43	0.29	−0.28	0.51	−0.41	−0.12
LNA	0.20	−0.47	−0.13	0.24	0.06	0.14	0.20	−0.01	−0.38
LMX	0.17	−0.33	−0.22	0.23	0.06	0.14	0.24	−0.04	−0.10
LFO	0.07	−0.03	0.44	0.10	0.42	−0.60	0.21	−0.46	0.34
LZA	0.20	−0.24	0.04	0.24	0.10	−0.02	0.20	0.10	0.36
LBC	0.22	−0.12	0.27	0.23	0.13	−0.10	0.27	−0.09	0.24
WRO	0.07	−0.05	−0.01	0.13	−0.09	−0.07	0.14	−0.43	−0.12
ICO	0.02	0.09	0.14	0.02	0.02	−0.11	0.03	−0.06	0.05
AZB	0.33	0.20	−0.02	0.25	0.01	0.31	0.27	0.18	−0.45
SBP	0.05	0.10	0.20	0.07	0.25	0.11	0.09	−0.11	0.03
LDI	0.26	−0.15	−0.08	0.21	0.21	0.22	0.19	−0.09	−0.06
LMT	0.06	−0.06	0.09	0.09	−0.12	−0.14	0.11	0.01	0.04
LPF	0.07	0.11	0.07	0.06	0.06	−0.00	0.10	0.03	0.14
BAM	0.05	0.24	0.19	0.04	−0.02	−0.03	0.04	−0.04	−0.09
BAB	0.19	0.39	0.23	0.17	0.08	0.36	0.17	0.02	−0.26

TABLE 7
(Continued)

Individuals, Males

% Total:	Age group 2 = 72.3%			Age group 3 = 58.0%			Age group 4 = 70.3%		
Var	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
HRO	0.08	−0.01	0.10	0.10	0.01	−0.08	0.11	−0.02	0.15
HMC	0.19	−0.11	−0.01	0.19	0.05	0.11	0.19	0.02	0.04
MHS	0.16	0.10	0.09	0.16	0.00	0.07	0.12	0.07	0.07
HBP	0.11	0.16	0.24	0.11	0.17	0.30	0.04	−0.03	0.28
GLD	0.36	0.13	−0.13	0.35	−0.14	0.03	0.30	0.19	0.11
LCP	0.39	0.35	−0.49	0.36	−0.50	−0.23	0.28	0.50	0.09
DHI	0.08	−0.02	−0.02	0.06	0.07	0.07	0.08	0.02	0.04
AHM	0.11	0.08	−0.05	0.16	−0.45	−0.07	0.13	0.13	0.10
PHM	0.21	0.11	−0.13	0.19	−0.16	0.17	0.16	0.46	0.18
% PC	59.1	7.2	6.1	40.0	9.5	8.5	56.7	8.7	4.9

Means, Females

% Total:	Age group 2 = 82.3%			Age group 3 = 69.5%			Age group 4 = 75.0%		
Var	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
GLS	0.37	0.16	−0.53	0.56	0.02	−0.13	0.43	−0.25	0.40
LNA	0.05	0.10	−0.02	0.31	−0.40	−0.12	0.22	−0.48	−0.03
LMX	0.03	-0.00	0.13	0.28	−0.30	−0.41	0.32	−0.45	−0.05
LFO	−0.00	0.23	−0.43	0.24	0.15	−0.07	0.09	0.07	0.66
LZA	0.11	0.16	0.26	0.19	0.14	0.14	0.21	0.37	−0.03
LBC	0.18	0.18	−0.13	0.42	0.11	0.12	0.24	0.30	−0.03
WRO	0.08	0.06	−0.06	0.16	−0.05	−0.05	0.14	0.22	0.12
ICO	0.06	0.05	−0.01	0.03	0.11	−0.07	0.08	0.08	−0.02
AZB	0.33	0.34	0.24	0.12	−0.10	0.15	−0.03	−0.01	−0.12
SBP	0.03	0.12	0.19	0.08	0.12	−0.09	−0.07	−0.03	0.13
LDI	0.19	0.07	−0.22	0.13	−0.03	0.09	0.29	−0.04	−0.10
LMT	0.13	0.06	−0.16	0.11	0.12	−0.03	0.04	−0.07	0.07
LPF	0.09	−0.01	0.10	0.12	0.16	0.04	0.11	0.08	0.01
BAM	0.07	0.20	0.06	0.03	0.05	−0.01	0.03	0.00	0.07
BAB	0.24	0.22	0.22	−0.04	0.62	−0.62	0.19	0.03	0.08
HRO	0.05	0.08	0.11	0.07	0.01	−0.07	0.09	0.15	0.09
HMC	0.17	0.07	−0.20	0.18	0.18	0.19	0.18	−0.03	0.12
MHS	0.14	0.14	−0.03	0.08	0.16	0.22	0.03	−0.03	−0.24
HBP	0.09	−0.02	0.06	−0.02	0.17	0.16	0.17	0.23	0.04
GLD	0.27	0.23	0.18	0.09	0.34	0.25	0.27	−0.04	−0.28
LCP	0.58	−0.72	−0.01	0.23	0.09	0.24	0.31	0.22	−0.16
DHI	0.04	0.02	0.07	0.14	−0.06	−0.02	0.12	0.16	0.07
AHM	0.13	0.08	0.13	0.07	0.07	0.01	0.20	0.17	−0.03
PHM	0.27	−0.07	0.27	0.03	0.07	0.28	0.28	−0.01	−0.37
% PC	40.1	33.9	8.3	36.9	18.0	14.6	40.3	19.3	15.4

Means, Males

% Total:	Age group 2 = 74.2%			Age group 3 = 89.4%			Age group 4 = 85.7%		
Var	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
GLS	0.19	0.45	0.33	−0.03	0.57	−0.11	0.43	−0.33	0.15
LNA	−0.12	−0.07	0.57	0.02	0.30	−0.24	0.22	−0.18	−0.15
LMX	−0.07	−0.19	0.50	0.01	0.25	−0.37	0.22	−0.15	−0.01
LFO	−0.04	0.44	−0.22	0.00	0.26	−0.01	0.17	−0.20	0.53
LZA	0.00	−0.15	0.05	0.03	0.21	0.16	0.26	0.02	−0.05

TABLE 7
(Continued)

	Means, Males								
% Total:	Age group 2 = 74.2%			Age group 3 = 89.4%			Age group 4 = 85.7%		
Var	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
LBC	0.20	0.17	−0.15	−0.00	0.42	0.12	0.22	−0.12	0.08
WRO	−0.03	0.06	0.16	−0.02	0.14	−0.09	0.12	−0.07	−0.20
ICO	0.02	0.13	0.03	0.00	0.03	−0.03	0.00	0.00	0.07
AZB	0.39	−0.15	−0.14	−0.03	0.13	0.02	0.20	−0.08	−0.51
SBP	0.06	0.21	0.16	0.01	0.10	−0.08	0.07	−0.02	0.02
LDI	0.22	−0.08	0.18	0.01	0.14	0.03	0.17	−0.08	−0.30
LMT	0.07	0.23	0.04	−0.00	0.11	0.04	0.14	−0.04	0.18
LPF	−0.04	0.12	0.24	−0.01	0.11	0.08	0.13	−0.02	0.04
BAM	0.12	0.33	0.02	−0.02	0.02	0.00	0.01	0.00	0.41
BAB	0.36	0.29	0.05	−0.01	0.07	0.08	0.16	−0.06	−0.07
HRO	0.05	0.11	0.12	−0.00	0.08	−0.03	0.08	−0.04	0.06
HMC	0.15	−0.13	0.05	−0.00	0.18	0.17	0.19	0.04	−0.12
MHS	0.20	0.03	−0.06	0.01	0.09	0.21	0.13	0.03	−0.04
HBP	0.16	0.05	0.09	−0.01	−0.02	0.15	0.07	−0.01	0.16
GLD	0.42	−0.21	−0.06	−0.12	0.07	0.74	0.36	−0.02	−0.02
LCP	0.42	−0.15	0.06	0.03	0.25	0.24	0.36	0.19	0.05
DHI	0.05	−0.03	0.06	0.23	0.12	−0.07	0.08	−0.00	0.08
AHM	0.11	0.03	0.13	0.52	0.03	−0.08	0.15	0.36	0.09
PHM	0.24	−0.22	0.07	0.81	−0.03	0.09	0.27	0.76	0.03
% PC	45.1	18.0	11.1	74.1	9.4	5.9	69.7	11.1	4.9

geographicaly closer GLs in some age and sex groups (M-X-A, A-X, M-I, M-I-D, O-E, V-M, P-N-L, P-N, P-L). From these, the most consistent were GLs A-X in all specimens, except for old males (age group 4). However, shorter phenetic distances were most common among GLs geographically separated. Such groupings were not consistent in all age and sex groups (fig. 4).

Cluster Analysis

In the cluster analysis using only subadult (2) and adult (3) specimens from the same 12 GLs (A, B, C, E, I, L, M, O, P, R, X, and Y), the localities clustered in several different subgroups according to age and sex. Such clusters were not related to the geographic nearness of the samples in every case (fig. 5). The phenogram with the highest cophenetic coefficient was that of subadult males (2, r = 0.915) followed by those of the females of that age (2, r = 0.8728), adult females (3, r = 0.8345), and adult males (3, r = 0.8062).

Only the phenogram for subadult females could be compared to that of adult males (r =0.8519. fig. 5), since Mantel's tests resulted in r < 0.8 in the other cases (Rohlf and Fisher, 1968). In spite of this, certain common groupings were recognized among the four phenograms. The first case was a cluster including *T. u. albigularis* (A) and the pocket gophers from Sierra de Tlaxco (X) in adult females, as well as in the two male groups. Another group was formed by *T. u. tolucae* (O) with *T. u. orizabae* (R) in both adult females and subadult males. Note that in every phenogram, *T. u. pullus* (P) separated either from the rest (all of the females and adult males) or from the annexed subgroup (subadult males).

The clusters in figure 5 do not coincide completely with each other nor with the clusters in figure 4 depicted by discontinuous lines. In the latter, cluster analyses were run using all the GLs available for each age and sex group. Cophenetic coefficients (r) were 0.93 for young females, 0.83 for adult females, and 0.96 for old females. In males, r was 0.83 in young males, 0.90 in adult males, and 0.75 in old males.

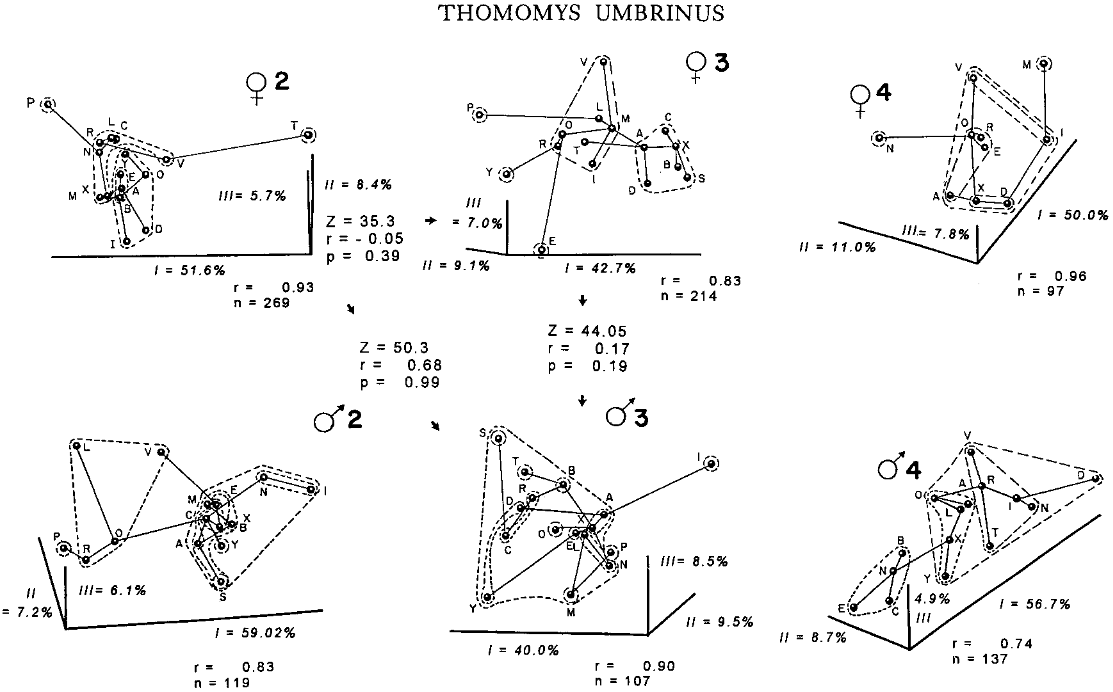


Fig. 4. Distribution of populations of *Thomomys umbrinus* along the Mexican Transvolcanic Belt in multivariate space, according to sex (♀/♂) and age (2–4). Notice that *Thomomys umbrinus pullus,* when present, always separated from other samples and that the position of the samples is variable in each sex and age. Axes and spheres indicate the position of group localities with respect to Principal Components Analyses computed on the population means. Lines connecting group localities result from a Minimum Spanning Tree projected onto the first principal components (I-III). Percentages refer to the amount of variation explained by each principal component. Discontinuous lines indicate groups according to Cluster Analyses developed in the sample means (r = cophenetic coefficient for the phenograms; n = sample size). Mantel's Z tests (r = correlation; p = significance) and arrows indicate comparability between phenograms. See names of group localities (letters) in table 1. Diagrams were drawn with the same scale and are rotated to different degrees for the sake of clarity.

For consistent groups, this cluster analysis coincided with the MST and PCA, except for some GLs that formed different arrangements. In young females, GL V clustered within the group formed by GLs C-L, N, R, X, and M, instead of linking with GLs Y and T, which in turn were clustered within different groups. In adult females, GL T grouped with GLs I-M, O-R, L, and V, instead of grouping within the cluster including GLs A-X, C, S, B, and D. In old females, GLs I and V clustered closely together instead of gathering in separate groups (I, M, D, and V, O, R). In young males, the phenogram coincided perfectly with the MST. In adult males, GLs D-Y cluster closely instead of gathering with GLs A and E, respectively. In old males, the analyses were coincident, except for the shorter distance between GL D and GLs I-M implied in the MST.

CLASSIFICATION DISCRIMINATORY ANALYSIS

Table 8 shows the total number of specimens examined, as well as the percentages of correct classification according to their taxonomic designation or according the GL of origin. A total of 273 (74.2%, n = 368) males and 416 (71.1%, n = 585) females were correctly classified. All males from GLs P, L, T, D, Y, and S were completely classified, as well as females from GLs, P, Y, and S. Percentage of incorrectly classified females ranged from 50% in GL T to 4.4% in

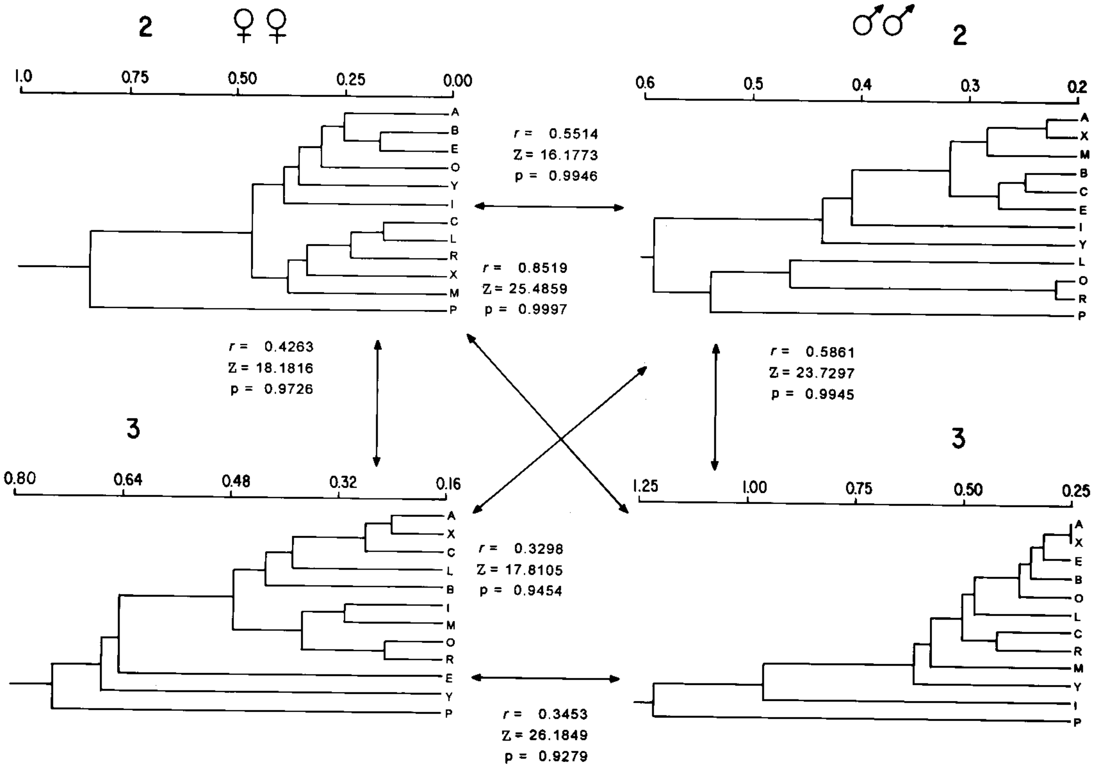


Fig. 5. Clustering of 12 populations of *Thomomys umbrinus* along the Mexican Transvolcanic Belt, according to sex (♀♀/♂♂) and age (2, 3). Arrows show the comparisons of the phenograms using Mantel's Z tests (r = correlation; p = significance). Cophenetic coefficients are r = 0.8728 in ♀2; r = 0.8345 in ♀3; r = 0.9150 in ♂2; r = 0.8062 in ♂3.

GL V, while males ranged from 46.5% in GL A to 12.4% in GL V.

Most of the GLs with larger sample sizes had more degree of misclassification (X, A, I, and O in females; A, O, and X in males) and females had a greater number of wrongly classified individuals than males. Misclassification in females occurred in 82.3% of all GLs (n = 14) and varied from one (GLs T and V) to 13 (GL X) with an average of 5.1 GLs. GLs C, I, O, A, and X had wrongly classified females in more than one-third of the total number of GLs. In males, misclassification occurred in 64.7% (n = 11) of the GLs, fluctuated from two (L and M) to 10 (GL X) GLs, and averaged 5.2 GLs. GLs E, O, A, and X also had wrongly classified individuals in more than one-third of the examined populations.

Similarly, more than being related to the geographic distribution of the GLs, the degree of overlapping of a certain GL is also related to sample size: the larger it is, the greater the overlapping (table 8). In general, except for the GLs P and D in males, GLs overlapped through poorly classified specimens. In the extremes, GL V (males, 3.4%; females, 4.4%) showed the lowest overlapping percentages and GL T (males, 90.0%; females, 66.7%) the highest. In females, overlapping of a GL with the others varied from one (GL P) to eight (GL O) but the average number was nine GLs (52.9% of the total number of GLs). Overlapping in males ranged from one (GLs V and M) to six (GL L) and the average was four GLs (23.5% of all GLs).

COLOR

Since color was not included in the analyses but has been cited frequently in the literature, some detailed notes on color are included here. In general, color does not correlate well with the taxonomic designations of specimens at UAMI. However, from a superficial qualitative analysis of the soil extracted from the claws of some specimens, it was noted the hair shade might be related to the color of habitat soil. In areas where soil is yellowish since it contains more clay, specimens tend to be Clay 26, Tawny 38, Cinnamon 39, or Cinnamon Rufous 40. In darker soils with a larger amount of humus, specimens tend to be Vandyke Brown 121, 221. In specimens from darker soils with volcanic sand, specimens are also Vandyke Brown 121, and they can be Blackish Neutral Gray 82. All of the shades described are bright in specimens with shiny and, occasionally, greasy pelage but can be dull in others, especially in clay and sandy soil.

Thomomys umbrinus albigularis (A). The holotype and topotypes show regular ochraceous coloration (Colors 26, 38, 39 and 40), on the whole back in the older specimens, but in the younger ones, the color shade tends to become darker toward the middle line (Color 121). Five of the six examined specimens showed a white tail tip. The backs of the hands and feet were white. The ventral coloration is lighter and blends with gray shades (like ‘‘dirty sand’’). The hair base is Medium Plumbeus 87 and the distal half shows the described shade or it is white. The white spot on the throat and the internal skin of the cheek pouches are also white. The hair is silky and bright.

Thomomys umbrinus martinensis (M). The cranium of the holotype had one printed label with the name of *Thomomys umbrinus sheldoni* and a handwritten label, by E. W. Nelson, with the name of *Thomomys umbrinus peregrinus*. The skin is very deteriorated and the colors are mixed. In general, it is like that of *T. u. albigularis*, with molting indication in different brown shades. Coloration is lighter (Cinnamon 39) on the coccyx area and on the flanks and darker (Tawny 38) on the head, back, and lumbar region. Because of the exposure of the hair base which is plumbeous gray (Color 87), the flanks show a light and grayish brown. From the waist to the anterior extreme and on the middle line, the holotype lacks hair. The tail and the ventral skin are as in *T. u. albigularis* and it shows a white stripe on the neck. The skin in the cheek pouches is whitish. It could seem either a young specimen from this subspecies which is molting or one of the lightest colored from *T. u. peregrinus*, *T. u. tolucae* or *T. u. umbrinus,* except that the color of the sides is brighter and more obvious. The other topotypical specimen is even younger and with molting evidence as well; thus coloration from its head down to the waist is dark and grayish. It has a very conspicuous round, ocher brown (Color 39) spot on the lower half of the left leg. In general, the hair transition goes toward the reddish ochre (Color 38), lighter on the flanks. The ventral hair is like that of *T. u. albigularis* and white appears on the throat, inside the cheek pouches, and on the back of hands and feet. The hair is greasy.

Thomomys umbrinus orizabae (R). The holotype is a melanistic specimen with a black matte shade (Color 82) and very dark brownish glittering areas on the head and middle line of the body (Color 121). It shows molting from the coccyx to the base of the tail where it has wooly juvenile hair. The dark color becomes lighter toward the flanks where it becomes ash black (Color 82). In contrast, half of the back of hands and feet as well as two-fifths of the tail are white. As in the flanks, the ventral pelage is also ash black (Color 82), but dark brown (Color 121) on the mammal gland areas and where the thighs begin. The mouth perimeter, the throat and the cheek pouches are white. Melanism is also present among the 14 topotypes, but two specimens, which show evidence of molting from head to waist, are ochre brown color (Color 26, 39), like *T. u. albigularis* or *T. u. tolucae*. All of the melanic specimens show a lighter hair base (Color 87) and darker at the tips (Color 82), as well as the contrasting white color on the back of hands, feet and the tip of the tail. Five specimens show a small white spot on the throat, and, except for one, all have white on the inside skin of their cheek pouches. The ventral skin of the light specimens is as in *T. u. albigularis*. In the melanistic ones, it is plain gray (Dark Neutral Gray 83), and a little bit lighter in both scapular and pelvic areas (Medium Neutral Gray 85).

TABLE 8

Morphometric Overlap Among 17 *Thomomys umbrinus* Populations in the Mexican Transvolcanic Belt, According to Taxonomic Designation

Group localities are mentioned from west to east (see table 1 for names). In the last two rows Σ indicates the total number of individuals considered as belonging to a certain taxon and tn refers to the total number of overlapping individuals for each case. The last column shows the number of specimens examined. Numbers within each cell indicate number of specimens and the percentage represented. Number of individuals and percentage of correct classification in the original sample appear along the diagonal in bold face.

Females

	P	N	B	L	O	T	C	E	V	M	D	A	X	Y	I	R	S	n
P	**25** **100**																	25
N		**10** **83.3**			1 8.3								1 8.3					12
B			**14** **63.6**	2 9.1			1 4.5	5 22.7										20
L				**11** **73.3**			2 13.3		1 6.7			1 6.7						15
O		2 3.6	3 5.4		**39** **70.9**				1 1.8			2 3.6	1 1.8	1 1.8	1 1.8	4 7.3	1 1.8	55
T					1 50.0	**1** **50.0**												2
C		1 3.7	1 3.7	1 3.7	1 3.7		**19** **70.4**					1 3.7	1 3.7			2 7.4		27
E		1 3.6		3 10.7	1 3.6			**17** **60.7**		1 3.6							5 17.8	28
V					2 4.4				**43** **95.5**									45
M			1 12.5							**6** **75.0**							1 12.5	8
D						1 10.0				1 10.0	**6** **60.0**		1 10.0				1 10.0	10
A		1 2.1	3 6.4	1 2.1	1 2.1		6 12.8	3 6.4			2 4.3	**25** **53.0**	1 2.1		3 6.4	1 2.1		47
X	3 1.6	8 4.3	10 5.4	1 0.5	1 0.5		10 5.4	4 2.2		3 1.6	8 4.3	11 5.9	**119** **63.3**	1 0.5	1 0.5		5 2.7	185
V														**3** **100**				3
I		1 1.9	1 1.9			1 1.9		1 1.9		3 5.7		1 1.9	7 13.2		**38** **71.3**			53
R		3 6.8		1 2.3	2 4.5			1 2.3							1 2.3	**36** **81.1**		44
S																	**4** **100**	4
Σ	28	27	33	21	49	3	38	31	45	13	16	41	131	5	44	49	11	585
tn	3	17	19	9	10	2	19	14	2	8	19	16	12	2	5	13	7	177

Thomomys umbrinus peregrinus (E). The holotype shows a dark brownish shade (Color 121), darker on the cheeks, nose, forehead and dorsum down to the waist, but especially on the back. It has a slight white spot above the right ear. The color gets lighter toward the flanks, cheekbones and below the waist. The tip of the tail, back of the hands and feet are white. It has a darker shade than *T. u. albigularis* and its belly is more grayish and whitish, though yellowish (Straw Yellow 56). Similar to that of *T. u. albigularis*, the brown back in the topotypes goes from ochre (Color 38) to a dark shade (Color 121), but it is darker on the middle line. Moreover, the abdomen is not quite different and 11 out of

TABLE 8
(Continued)

Males

	P	N	B	L	O	T	C	E	V	M	D	A	X	Y	I	R	S	n
P	**15** **100**																	15
N		**7** **63.3**		1 9.1	1 9.1							1 9.1	1 9.1					11
B			**11** **84.6**				1 7.7	1 7.7										13
L				**7** **100**														7
O		1 3.1		1 3.1	**21** **65.0**	2 6.2	1 3.1	1 3.1	1 3.1				2 6.2				2 6.2	32
T						**3** **100**												3
C		1 7.7	1 7.7				**10** **76.9**										1 7.7	13
E			2 10.5	1 5.3		2 10.5		**12** **63.2**								1 5.3	1 5.3	19
V					1 3.1	1 3.1			**28** **87.5**					1 3.1		1 3.1		32
M										**12** **85.7**				1 7.1		1 7.1		14
D											**2** **100**							2
A				1 3.6	1 3.6	1 3.6	2 7.1	1 3.6				**15** **53.6**	2 7.1	1 3.6	4 14.3			28
X		6 3.2	2 1.1	3 1.6	2 1.1		1 0.5			2 1.1		8 4.3	**83** **70.9**	4 2.2	3 1.6		3 1.6	117
V														**5** **100**				5
I						2 7.7		1 3.8				1 3.8	4 15.4		**17** **65.4**	1 3.8		26
R				1 3.7				3 11.1				1 3.7		1 3.7		**21** **77.8**		27
S																	**4** **100**	4
Σ	15	15	16	15	26	11	15	19	29	14	2	26	93	12	25	26	9	368
tn		8	5	8	5	10	5	7	1	2		11	10	7	8	5	6	98

the 15 specimens examined showed the white spot on the throat. The tip of the tail tends to be white, as well as the back of the hands and feet. The shade of this gopher is among the darker ones (Color 38) of *T. u. albigularis,* and the lightest ones (Color 26, 39) of *T. u. orizabae.* Their hair is bright.

Thomomys umbrinus pullus (P). In the case of the specimens from Los Tanques, similar patterns to those described above were found, but intermingled. Thus, some melanistic specimens (Color 82) were observed, and others were dark brown (Color 121) as it was described for any of the subspecies with that shade. Their hair is bright.

Thomomys umbrinus tolucae (O). The holotype and topotypes show a general shade very similar to that of *T. u. peregrinus,* but with a duller shade (ash). The hair is greasy. The holotype shows a more grayish shade because it has lost a lot of hair and the gray (Color 84) base of hair is exposed at the abdomen. In other ways, it would look like *T. u. albigularis,* to which it is also similar in the shade of the cheekbones, outside of the forearms and especially, on both sides of the base of the tail. Five of the nine specimens examined show a white spot on their throat. In a few, the tail is white from the half and, in others, it is in the last third. Likewise, the skin on half the back of hands and feet and inside the cheek pouches is white.

Thomomys umbrinus umbrinus (S). The color of the topotypes is quite variable, since most are young. The darkest ones are similar to *T. u. tolucae* with a dull-ash shade, and the lightest ones to *T. u. albigularis*. In all of them, the distal half of the tail is white and they show the white spot on their throat. The white back of hands and feet is more evident than in *T. u. albigularis*. The ventral shade is as in *T. u. albigularis* or as in *T. u. peregrinus* or *T. u. tolucae*.

Thomomys umbrinus vulcanius (V). The holotype is dark ash brown (Color 121) due to the abundant gray undercoat hair (Color 85) which gives it a wooly texture. The back is dark brown (Color 121) becoming lighter on the flanks. The tip of the tail and the back of hands and feet are white. The ventral color is as in *Thomomys umbrinus peregrinus*. The mouth perimeter and the skin of the chin are white. The hair is greasy.

Thomomys umbrinus ssp. (C, X, I, T, B, Y). The same diversity of color patterns was found in the pocket gophers from elsewhere in the MTB and without taxonomic designation. Melanistic (Color 82) specimens are also found in *Thomomys umbrinus* ssp. from Sierra de Las Cruces (C) and those from the Sierra de Tlaxco (X). Among the latter, there are also individuals with the ochre brownish types (Colors 26, 38, 39, 40) and dark brown (Color 121), which can be shiny or ash. Other pocket gophers that show a darker brown (Color 121), as in *T. u. orizabae*, are those from Sierra de Tlaxco (X), Paso de Cortés (*T. u. vulcanius*, V), La Malinche (I), Totoltepec (T), and those from the Cerro de San Andres (N) and Sierra de Las Cruces (C). Among those that have a brown ash shade are specimens from La Malinche (I), Amanalco de Becerra (B), and Cerro de San Andres. Individuals that show an ocher brown shade (Colors 26, 38, 39 and 40), such as *T. u. albigularis*, are from La Malinche (I), Oyameles (Y) and Sierra de Tlaxco (X).

DISCUSSION

NONGEOGRAPHIC VARIATION

Genetic variation within a population can be seen as its fine tuning to habitat conditions in response to natural selection (Mayr, 1970). As a result, we assume that populations of the same species located in ecologically distinct habitats will show nongeographical differences in ontogenetic variation, sexual dimorphism, and other individual variables such as coloration, shape, and size. Therefore, the analysis of nongeographic variation is a preamble to the study of geographic variation (Ramírez-Pulido et al., 1991); but more importantly, it is one of the most accurate tools to understand the morphometric mechanisms involved in several aspects of the biology of populations (Owen and McBee, 1990; Patterson and Patton, 1990; Alves de Oliveira, 1992; Zelditch et al., 1992; Lovich and Whitfield Gibbons, 1992).

This is especially important in the case of *Thomomys umbrinus* (results shown here), *T. bottae* (Patton and Smith, 1990), and *T. townsendii* (Rogers, 1991a), since the high structural elasticity of their morphological features affects the expression of both ontogenetic variation and sexual dimorphism. Therefore, in these species as well as in others with the same characteristics, a poor knowledge of their intrapopulation variation could bias the results of interpopulation variation, and thus, make them useless.

In general, individual variation of *Thomomys umbrinus* from Sierra de Tlaxco, Tlaxcala (table 2) is similar to that found for other geomyids (Baker and Genoways, 1975; Hollander, 1990) and other rodents (Baumgardner and Schmidly, 1981; Stangl et al., 1991). However, CVs in this pocket gopher are of smaller magnitude and, thus, suitable for taxonomic comparisons (Long, 1969). Likewise, in this as in other species of geomyids (Grinnell, 1931; Davis, 1937, 1938; Wilkins, 1985; Rogers, 1991a) and rodents (Yancey et al., 1993), females show greater morphological uniformity than males. Eisenberg (1981) has suggested that morphological characteristics enable differential strategies between sexes related to the energy they devote to other biological processes (e.g., territoriality in males, gestation and nursing in females).

Age turned out to be the most important factor in nongeographic variation of *Thomomys umbrinus* from Sierra de Tlaxco (tables 3, 5, GL X). This pattern has also been found in *Mus musculus* (Straney, 1978) and other populations of *T. umbrinus* along the Mexican Transvolcanic Belt (unpublished data). In contrast, Smith and Patton (1988), Patton and Smith (1990), and Rogers (1991a) found that sexual dimorphism (tables 4, 5) is more relevant among adult and old adults in other species of *Thomomys*. It must be noted, though, that these authors *a priori* excluded younger classes from their studies, while we found separation among individuals from ages 2 to 4. Also, these authors followed a different statistical approach in order to increase sample sizes and their criteria for assigning individuals to age groups (Daly and Patton, 1986) are different from ours (Castro-Campillo et al., 1993).

With our approach, we found that both age and sex play an outstanding role in the nongeographic variation of *Thomomys umbrinus* from Sierra de Tlaxco. Indeed, they interact in one-third of the measurements (table 5). Therefore, it was decided to run the analyses on the geographic variation with separate age groups and sexes. Hollander (1990) arrived at a similar conclusion upon examining the variation of *Cratogeomys castanops*.

Interaction between sex and age (table 5) suggests a differential pattern of development between males and females (Castro-Campillo et al., 1993). In *Thomomys umbrinus* as in *T. bottae* (Patton and Smith, 1990), females seem to reach the proportions of the adult cranium sooner than males, which implies lower morphological variation among females than among males (Patton and Smith, 1990). This fact, which has been continuously observed in other pocket gophers, has favored the use of females in comparisons and descriptions of the taxa (Merriam, 1895; Bailey, 1915; Grinnell, 1931; Davis, 1937).

The difference between skull growth of males and females of the congeneric species *Thomomys bottae* has been given various interpretation by different authors. To Howard and Childs (1959), it implied that males continue to grow throughout their life. In contrast, for Patton and co-workers (Daly and Patton, 1986; Patton and Smith, 1990), it proves the proportional increasing loss of smaller sized individuals within the population. In the case of *Thomomys umbrinus*, it is necessary to carry out growth studies to arrive at any conclusion. It will not be surprising if males continue to deposit calcium in their skulls at an age when females have finished doing so and are losing that element through pregnancy and lactation as in other mammals (Bentley, 1998). Moreover, sexual differences in skull conformation might be caused by less opportunity for females to deposit calcium in their bones because of menstruation, as in human females.

Finally, we must note that the skull development of *Thomomys* has been related to extrinsic patterns (Bailey, 1915; Patton and Brylski, 1987); indeed, the great elasticity shown by these gophers is multifactorial (Smith and Patton, 1988; Lessa and Patton, 1989). Therefore, both ontogenetic variation and secondary sexual differentiation should be examined in depth, as done here, before studying geographic variation. Such scope will allow immediate factors, such as the environmental influence, to be considered separately from nonimmediate factors, such as evolutionary and adaptive processes developed throughout the phylogenetic history of these species (Patton and Smith, 1990).

GEOGRAPHIC VARIATION

Working with subspecies, and especially using morphometry, involves a careful interpretation of the existence of gene flow on the basis of phenetic similarity (Rogers, 1991a). Specimens assigned to each subspecies should be reasonably uniform (Pimentel, 1979; Manly, 1986). This supposition is not fulfilled in the analyzed populations, partly because of the different sample sizes.

The diversity of results in the multivariate analyses (figs. 3–5, tables 6, 7) may be caused, in part, by differing sample sizes, very small in some GLs (Oyameles, Totoltepec, *T. u. umbrinus*). However, it was decided to use all of the specimens to explore the phenetic similarity among the populations. Other authors (Smith et al., 1983; Smith and Patton, 1988; Hollander, 1990) have also included single specimens or very small sample sizes (n < 4) in analyses of patterns among geomyids, transforming the data into their logarithmic expression (Neff and Marcus, 1980; Rohlf and Bookstein, 1990). Homogenization of quantities is a useful strategy in cases where ‘‘all of the adult specimens’’ have been used. However, since adult specimens were separated here into six groups, according to age and sex classes, variability is divided and the results are less extreme (R. D. Owen, and R. O. Gonzalez-Robles, personal commun.).

Likewise, the use of six age groups resulted in a better expression of their geographic variation (i.e., high cophenetic coefficients in the cluster analysis or in the eingenvalues of the PCA, table 7). Moreover, splitting of variation indicates that in the PCA on the GL means (fig. 4, table 7), PC I was a factor of shape (i.e., eigenvalues of different signs and some variables distinctly heavier than others; Pimentel, 1979; Neff and Marcus, 1980) and not exclusively of size, as is usually the case.

Results of classification discriminant analyses of variables (table 7) confirm the general pattern found in the rest of the analyses (tables 6–7, figs. 3–5) in terms of a general overlap among populations. Indeed, although discrimination accuracy was good (> 70%), population sample size had a more definite influence, since all of the GLs with n < 10, except for Totoltepec (GL T), are better classified. However, these specimens, except for *T. u. pullus,* also overlapped more with other larger samples. Indeed, the greater the sample size, the larger the overlap with other small and large samples.

The fact that in *Thomomys umbrinus,* male dimensions from different localities overlap less than female dimensions, confirms that the latter are morphometricaly more uniform (Castro-Campillo et al., 1993) among GLs (table 8). This is a phenomenon also demonstrated in other species of the genus (Grinnell, 1931; Davis, 1937; Patton and Smith, 1990; Rogers, 1991a) and in other genera of pocket gophers (Davis, 1940; Honeycutt and Schmidly, 1979; Wilkins, 1985; Hollander, 1990). As mentioned before, this can be related to different sexual roles (Eisenberg, 1981; Castro-Campillo, et al., 1993). To confirm this, it will be necessary to carry out both ethological and ecological studies in situ, as well as physiological studies.

Overall, with the exception of *T. u. pullus,* results of multivariate analyses also show no definite pattern attributable to geographic distribution (figs. 3–, table 6). Different GLs are grouped together regardless of geographic distance between them according to the sex and age considered in the analysis. The only taxon consistently segregated in every analysis, when it is present, is *T. u. pullus*.

The absence of a common pattern and the diversity of combinations of GLs in multivariate space (figs. 3–5) may suggest different factors in the association of individuals in the different ontogenetic and sexual groups. It also may suggest that chance and small sample sizes are important. These results can be interpreted as a structural homogeneity referable to shape and size. Size is the most important characteristic to distinguishing *T. u. pullus* from the rest.

Rogers (1991a) also found morphometric homogeneity in *Thomomys townsendii,* in which she examined nine subspecies in four states of the United States. Since size was very important in her analysis, she decided to interpret her results with caution because Patton and co-workers have shown that in *Thomomys bottae,* size depends on ecology (Straney and Patton, 1980; Smith et al., 1983; Kennedy and Lindsay, 1984; Daly and Patton, 1986; Patton and Brylski, 1987; Patton and Smith, 1989, 1990). After examining the genic variation of *Thomomys townsendii,* Rogers (1991b) concluded that there are two and not nine subspecies.

After examining 43 subspecies of *Thomomys bottae* in California, Patton and Smith (1990) found that cranial size is a character that responds in a very plastic way, and that therefore, shows great variation. They interpreted this to mean that size is related to nongenetic effects such as nutrition and other environmental factors. In contrast, shape expresses allometric differences in the mensurable characters; according to Smith and Patton (1988) it is more useful in defining regional geographic units, even though certain specific morphologies are recurrent along the species range. From biochemical analyses, these authors have found an inverse relationship between the magnitude of genetic distance and geographic distance (Smith et al., 1983). Based on their findings, and with a conceptual modification of Grinnell's criteria (1935) for the recognition of the subspecies, Smith et al. (1983) recognized 15 infraspecific entities of *Thomomys bottae* in California.

In the case of *Thomomys umbrinus*, the extensive overlap revealed in the ANOVA and most of the multivariate analyses (figs. 3, 4, table 8), demonstrates that skull shape of this species exhibits no clear geographic pattern along the MTB. The only exception is *T. u. pullus*.

Davis (1938) noted that the skull of *Thomomys bottae* and *Thomomys quadrattus* (a current subspecies of *T. talpoides*) is larger in populations inhabiting lower altitudes and deeper soils. In contrast, the skull is smaller in those populations found in high altitudes, where the ground is shallower (Davis, 1938). Besides size, Davis (1938) mentioned the same relationship in the presence and conspicuousness of the skull crests (sagittal, lambdoid, and temporal crests), and he considered it inappropriate to designate a trinomial on the basis of these crests. Davis (1938) concluded that variation within the species examined, together with the recognition of the topography and geological history, was sufficient to determine the validity of a subspecific entity. Choate and Williams (1978) reached a similar conclusion in the interpretation of variation in *Microtus ochrogaster*.

Davis's conclusions (1938) make sense for *Thomomys umbrinus pullus*, since the skull is smoother and smaller in this subspecies, a fact possibly related to the depth of the soil and to a less intricate topography of its habitat (Pasquaré et al., 1987a, 1987b). To a lesser degree, the differences found in *T. u. pullus* can also be related to the geological history of its distribution area (Demant, 1978, 1982; Nixon et al., 1987; Pasquaré et al., 1987b).

Further evidence of cranial homogeneity in *Thomomys umbrinus* from the Mexican Transvolcanic Belt is that all populations located east of Pátzcuaro, Michoacán, show recurrent shapes even when they are separated by more than 100 km. Such is the case of populations from Amanalco de Becerra (GL B) and La Malinche (GL I). This has been interpreted as canalization within a fossorial niche (Honeycutt and Schmidly, 1979; Lessa and Patton, 1989) and, thus, is given less weight than the allometric patterns in defining infraspecific entities (Patton and Smith, 1990).

With respect to pelage coloration, there is overlap regardless of taxonomic designation or geographic location. Moreover, examination of the holotypes and topotypes makes clear that color discrepancies, rather than being diagnostic features, are conditions related to age of the specimen, the presence of molting, and the small number of specimens examined. Interestingly, the larger the sample size, the more color types are found: as in pocket gophers from Sierra de Tlaxco (GL X), *T. u. albigularis* (A), and *T. u. pullus* (P). Color patterns were not considered in the original descriptions or in the group reviews (Bailey, 1915; Nelson and Goldman, 1934; Hall and Villa, 1948). In *Thomomys umbrinus*, as in other pocket gopher species, different color types are not useful in characterizing taxonomic entities, which may share different color types in the MTB. Therefore, coloration in such species may not be a useful diagnostic feature; rather, it is related to the color and content of the soil (Davis, 1937; Rogers, 1991a; Patton and Smith, 1990).

In summary, results support the distinction of two subspecies (sensu Grinnell, 1935; Mayr, 1969) of *Thomomys umbrinus* on the southern boundary of its distribution. One of these, *Thomomys umbrinus pullus*, includes the populations in the surroundings of Patzcuaro, Michoacán. The other includes all of the other populations eastward from Sierra de Las Cruces, Michoacán, to the Pico de Orizaba Volcano, Veracruz. This second taxon, which includes several subspecies formerly recognized, as well as populations without previous designation, should be referred to *Thomomys umbrinus umbrinus*, the oldest name available. However, it is necessary to check the situation of this name, since the designation of the specimens of Boca del Monte is not very clear (Bailey, 1906), and the neotype(?) assigned to it was lost (D. Wilson, personal commun., November 1990).

Acknowledgment of two subspecies instead of eight in the Mexican Transvolcanic Belt agrees in general with the biochemical and cytological evidence found by Hafner et al. (1987). They showed that the *Thomomys umbrinus* specimens examined in the Mexican Transvolcanic Belt belong to the same cytotype (FN = 78) and that the genic differences between them are minimal (in fact, they place them in the same electrophoretic group). Likewise, Hellenthal and Price (1984) have found specific associations of ectoparasites shared by all of the *Thomomys umbrinus* specimens examined in the Mexican Transvolcanic Belt, as opposed to those located a few kilometers north.

Perhaps relationships found among populations of *Thomomys umbrinus* in the Mexican Transvolcanic Belt can be explained by the geological history of the Quaternary Age of the area, which also explains populations of other species of the genus (Davis, 1937; Rogers, 1991b). While the formation of the Mexican Transvolcanic Belt goes beyond the late Miocene (Cebull and Shurbet, 1987; Nixon et al, 1987), the origin of vulcanism in the region began during the Pliocene (Demant, 1978; 1982; Nixon et al., 1987). On the other hand, it is known that the Geomyidae originated in the late Miocene (Kurtén and Anderson, 1980), but the oldest records of the species in México are referable to the Late Pleistocene (Barrios Rivera, 1985). Some of these fossil records are found within the study area at Tequixquiac (Hibbard, 1955) and Tequesquinahua (Alvarez, 1966), both in the State of México.

In retrospect, one can visualize a large zone along the valleys of México, Toluca, and Pachuca having a homogeneous environment, with both climate and vegetation similar to those inhabited by the recent pocket gophers. This area was then reduced and partitioned by the changes in climate during the Quaternary Period (Hibbard, 1955). Moreover, at the end of the period, the rise of the strato-volcanoes in the central and eastern region of the Belt, less than one million years ago (Demant, 1978, 1982), separated *Thomomys umbrinus* populations.

Evidence of a larger duration of the climatic and ecological conditions is the fossiliferous locality of Tequesquinahua, a site 3.2 km northeast of Tlalnepantla (Alvarez, 1966). Even though xeric species of plants are currently found there, in the past, Tequesquinahua may have been covered by coniferous forests and grassland, because remnants of *Thomomys umbrinus* and *Neotomodon alstoni* were found there (Alvarez, 1966). Also, the fossil site at Tequixquiac, near Zumpango in the State of Mexico (Hibbard, 1955), has similar characteristics to Tequesquinahua; specimens of *Thomomys umbrinus* from the Pleistocene have been reported there (Hibbard, 1955).

Differentiation of *Thomomys umbrinus pullus* could be related either to this overall picture or to the nature of the soil that it inhabits. That is, this subspecies lives in a region with less deposition of volcanic sand than in areas of other populations (Pasquaré et al., 1987a, 1987b).

CONCLUSIONS

Both sexual dimorphism and, especially, age variation are important determining factors in the variation of *Thomomys umbrinus*. Such variation seems to be linked to a very fine tuning between ontogenetic development and sexual roles.

Analyses of geographic variation demonstrate that, except for *Thomomys umbrinus pullus*, previously recognized subspecies and other populations in the MTB are morphometrically similar regardless of their geographic origin. This finding does not support systematic recognition of eight subspecies in that region, despite some degree of geographic isolation. Besides, isolation among type localities is less than previously supposed, as shown by specimens obtained from intermediate localities.

Hence, we recognize *Thomomys umbrinus pullus* and the nominal subspecies as the only two subspecies of *Thomomys umbrinus* occurring in the MTB. The nomenclature may be summarized as follows:

Thomomys umbrinus umbrinus (Richardson)

1829. *Geomys umbrinus* Richardson, Fauna Boreali-Americana 1: 202, type locality undefined. Bailey (1906: 4) restricted the type locality to southern México, probably in the vicinity of Boca del Monte, Veracruz. GENERAL DISTRIBUTION: Veracruz.

1893. *Thomomys umbrinus orizabae* Merriam, Proc. Biol. Soc. Washington 8: 145, type locality: Mt. Orizaba, 9,500 ft, Puebla. GENERAL DISTRIBUTION: Puebla.

1893. *Thomomys umbrinus peregrinus* Merriam, Proc. Biol. Soc. Washington 8: 146, type locality: Salazar, 10,300 ft, México. GENERAL DISTRIBUTION: Distrito Federal, Hidalgo, México, and Morelos.

1934. *Thomomys umbrinus albigularis* Nelson and Goldman, J. Mammal. 15: 106, type locality: El Chico, 9,800 ft, Sierra de Pachuca, Hidalgo. GENERAL DISTRIBUTION: Hidalgo, Puebla, and Veracruz.

1934. *Thomomys umbrinus martinensis* Nelson and Goldman, J. Mammal. 15: 108, type locality: San Martin Texmelucan, 7,400 ft, Puebla. GENERAL DISTRIBUTION: Known only from type locality.

1934. *Thomomys umbrinus tolucae* Nelson and Goldman, J. Mammal. 15: 109, type locality: Northern slope of Toluca Volcano, 9,500 ft, México. GENERAL DISTRIBUTION: México.

1934. *Thomomys umbrinus vulcanius* Nelson and Goldman, J. Mammal. 15: 109, type locality: Popocatépetl, 12,900 ft, México. GENERAL DISTRIBUTION: México, Morelos, and Puebla.

Thomomys umbrinus pullus Hall and Villa

1948. *Thomomys umbrinus pullus* Hall and Villa, Univ. Kansas Publ. Mus. Nat. Hist. 1: 251, type locality: 5 mi S Pátzcuaro, 7,800 ft, Michoacán. GENERAL DISTRIBUTION: Known only from the vicinity of type locality.

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